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INFLUENCE OF SOIL TEMPERATURE AND MOISTURE ON THE DEVELOPMENT OF THE SEEDLING-BLIGHT OF WHEAT AND CORN CAUSED BY GIBBERELLA SAUBINETII[1]

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INTRODUCTION

Various seedling-blights, rootrots, and damping-off troubles of plants have long been associated with unfavorable soil and weather conditions. The soil-inhabiting organisms which cause this group of relatively obscure diseases usually become aggressive parasites only when the seedling or plant is weakened through its inability to react favorably to the environment. Plant pathologists are continually being reminded of the important correlation between climatic conditions and the occurrence of plant diseases. The fact is emphasized by Duggar (*10*),[2] Smith (*28, p. 36 et seq.*), and Jones (*21*) that the most important, most complex problems for long-time research include the critical study of the relation of environment to parasitism.

From the field standpoint, this problem was well illustrated in Illinois during the fall of 1919. The first part of the period for sowing winter wheat was hot and dry, followed later by cool, wet weather. The early sowings of wheat were made, therefore, in a comparatively warm and dry soil, whereas the later sowings were made in a cool and moist soil. In many of the early sown fields, the seedling-blight caused by the conidial stage of *Gibberella saubinetii* (Mont.) Sacc. destroyed more than half of the young seedlings. Chiefly on account of these ravages, together with Hessian fly injury, the stand and vigor were so greatly reduced that a number of such early sown fields were resown the following spring. In contrast to this, in the fields sown late in the autumn it was almost impossible to find a blighted seedling, even in the worst-infested fields.

These conditions are analogous to those affecting the development of cabbage yellows as noted by Gilman (*11*). Experiments show conclusively that the soil organism *Fusarium conglutinans* Wollenw. is capable of inducing cabbage yellows only at soil temperatures of 17° C. or above. Tisdale found that flaxwilt (*Fusarium lini* Bolley) developed

[1] Accepted for publication May 10, 1922. The investigations upon which this paper is based were conducted cooperatively by the Office of Cereal Investigations of the Bureau of Plant Industry and the Wisconsin Agricultural Experiment Station.

[2] Reference is made by number (italic) to "Literature cited," pp. 869-870.

only at soil temperatures above 16°. These observations and experiments tend to confirm Wollenweber's (*34*) generalization that the root-invading Fusariums are warm-soil organisms.

The Fusarium seedling-blight of wheat and other cereals (*Gibberella saubinetii*) has proved to be well adapted to a critical study of the relation of environment to parasitism, as the same parasite is able to attack a number of different host plants, especially wheat and other small grains and corn. The field observations on winter wheat, mentioned previously, indicate that soil temperature and soil moisture are important factors in the development of the disease. As a result of the suggestions from these field observations and the apparent importance of the diseases on both wheat and corn, investigations were undertaken to determine the relation of soil temperature and soil moisture to the development of seedling-blight of wheat and corn caused by *G. saubinetii*. The responses of the two hosts, wheat and corn, were so markedly different that the studies are being continued with the view of determining the physiological and chemical responses which determine host susceptibility. Although the results here presented are not complete, it is believed that they will serve to show the relation of temperature and moisture to the development of the blights caused by this one organism.

SEEDLING-BLIGHT OF WHEAT

The seedling-blight of wheat was not connected with the headblight or scab described by Smith (*29*), Weed (*33*), Chester (*8*), Arthur (*3*), and Hickman (*16*), until Selby and Manns (*27*) described the diseased seedlings obtained by sowing scabbed kernels. The seedling-blight has been mentioned since, and its close association with unfavorable weather conditions has been suggested by Bolley (*6*, *7*), Schaffnit (*25*), Akerman (*1*), Atanasoff (*4*), and others. This disease is prevalent in the winter-wheat areas of the Mississippi Valley. The losses from this stage of the disease vary greatly from year to year, depending upon climatic conditions.

The symptoms of the seedling-blight caused by *Gibberella saubinetii* vary, depending upon the portion of the seedling attacked and the environing conditions during the development of the blight. In case of severe attacks many of the germinating seedlings may be killed before they emerge, which results in reduced stand. When the attacks are less severe the seedlings emerge and are weakened or killed, according to the severity of the attack. Such seedlings, when carefully removed from the soil before disintegration, show all gradations of attack (Pl. 1 and 2). In many cases the developing embryo is invaded and killed before either roots or plumules elongate (Pl. 3, B). The embryo as well as the invaded portions of the kernel become reddish brown to carmine red as the soil-moisture condition varies from dry to wet. The fungus growth tends to accumulate over the surface of the infected tissues, causing the soil to cling tightly to the diseased parts.

In other instances, the plumule is blighted when less than 1 cm. long, the root development continuing, however, for some time afterwards (Pl. 1, *b*, and 3). Often the roots develop to a length of 5 to 10 cm. before they are invaded by the fungus. The invasion usually occurs by the parasite growing from the invaded endosperm into the proximal portions of the roots, after which the entire root is invaded and rotted. Other seedlings do not succumb to the attack until the first-leaf or often the

second-leaf stage. The attacked plants first become dwarfed and chlorotic, then wilt (Pl. 1, *c*), and finally fall over and become overrun by the parasite (Pl. 3, B). This latter stage is a typical wilt of the young plant. The old seed and the portion of the stem below ground develop the characteristic reddish brown color. Usually perithecia form gregariously on the culm near the soil line. Still other seedlings partly succumb to a root attack. In many cases all of the roots may be badly rotted and the plant considerably dwarfed. Such plants, when weather conditions are favorable for the development of the seedling, may send out new roots from the first node and entirely or partially recover (Pl. 2, *a*, and 3, A).

In many instances the reddish brown lesions occur only on the coleoptile without penetrating deeper into the tissue. The symptoms under these conditions are very similar to the same type of lesion produced by light attacks of Helminthosporium; the color in the former lesion, however, generally is slightly lighter.

SEEDLING-BLIGHT OF CORN

The relationship between seedling-blight and rootrot of corn and wheat scab caused by *Gibberella saubinetii* was earlier suggested by Arthur (*3*) and later proved by Hoffer, Johnson, and Atanasoff (*17*). This organism causes heavy losses in corn through the central and upper Mississippi Valley. In 1920, fields were reduced 10 to 25 per cent where corn was planted on fields in which the wheat crop, heavily infected with scab, had been plowed under the previous fall, while field inoculation experiments the same year demonstrated yield reductions of 10 to 30 per cent. Although the distribution and prevalence of this parasite on corn has not been definitely determined, yet it is evident that the organism is capable of causing heavy losses in the corn crop as well as in wheat.

The symptoms of the seedling-blight of corn caused by *Gibberella saubinetii* vary, as do those of wheat, depending upon the severity of attack, the age of the seedling, and soil conditions. As in the case of wheat, the corn seedling may be attacked in various stages, the type of infection being similar to that in wheat (Pl. 4, A, B, C). The lesions are more definite on the corn seedling, however, and usually extend from the kernel into the tap root and lateral roots as well as into the mesocotyl.[8] The invaded areas are at first light brown, water-soaked regions, soon turning reddish brown. The kernel turns reddish brown to carmine red, depending upon soil moisture conditions. The type and color of the lesion, as well as the color of the infected kernel, are distinctly different from similar infections produced by *Helminthosporium* sp. or *Diplodia zeae* (Schw.) Lev. The badly infected seedlings become yellow and wilt down in a manner very similar to that described for wheat. Many of the plants partially recover by sending out new roots and make a fair growth, although a rather high percentage of such plants fail to produce marketable ears.

The symptoms of the seedling-blights of corn caused by *Gibberella saubinetii* are in general very similar, the chief difference being the development of a more definite lesion on the larger stem and roots of corn. The symptoms on both hosts are variable, depending as they do upon many varying factors.

[8] The term "mesocotyl," as used in this paper, follows previous usage for corn, applying to the structure between the attachment of the scutellum and the base of the coleoptile.

The period of severe infection in both wheat and corn is usually restricted to the seedling stage. Few new infections occur after the seedling has reached the fourth-leaf stage. Occasionally, however, under weather conditions favorable for the development of the disease new root lesions may develop, which tend to reduce the vigor of the plant but rarely develop sufficiently to kill it.

LIFE CYCLE OF THE ORGANISM IN RELATION TO THE PRODUCTION OF SEEDLING-BLIGHT

The seedling-blight of wheat and corn develops from two chief sources; first, scabbed or infected seed and, second, infested soil. Floral infections in wheat develop during moist, warm weather and result in blighted or scabbed kernels within the infected spikelets. The mycelium hibernates in or on the scabbed kernels, many of which show no marked external symptoms until the seed is sown, when the parasite develops in the young seedling. Seed infection also occurs in corn. The mycelium hibernates in the seed and develops in the young seedling in the spring, following germination.

In addition to seed infection, the organism develops as a saprophyte on decaying crop refuse near or on the surface of the soil. It becomes aggressive as a parasite only when the seedlings are weakened by unfavorable environment.

EXPERIMENTAL METHODS

CULTURE METHODS

The temperature and moisture studies were conducted under controlled conditions in the greenhouse as well as under field conditions. Pure-line Marquis wheat (Wis. Ped. No. 50) was used in all of the spring-wheat studies and pure-line Turkey wheat (Wis. Ped. No. 2) was employed in the winter-wheat studies. Specially selected ears of Funk Ninety-Day yellow dent and Golden Glow yellow dent were used in all of the experiments. Only kernels free from disease and treated with mercuric chlorid 1 to 1,000, followed by rinsing, were used for inoculation and controls. In addition, naturally infected, scabbed wheat kernels were used in several experiments in comparison with artificially inoculated seed.

In the greenhouse the soil-temperature experiments were conducted in the Wisconsin soil-temperature tanks, considerably modified from those described by Jones (*21*) and Johnson and Hartman (*20*). The tanks, as constructed on the unit plan, consisted of the insulated water bath equipped with a rigid cover through which the soil containers were suspended in the water bath below.

Containers of two different sizes were used. A can 6 inches in diameter by 12 inches deep was used for most of the seedling studies, and a larger can 12 inches in diameter by 20 inches deep for the plant studies. In addition to being utilized as soil containers these larger cans were fitted with covers and used for culture chambers. These, together with the Altmann incubator, were used in the studies on the relation of temperature to the development of the fungus.

The water within the tank was heated by an electric heater in a watertight copper container submerged at the bottom of the tank. The heater was controlled by a mercury thermostat set in the water bath and an

ordinary telegraph relay. The temperatures below greenhouse temperature were maintained by running a stream of cold water into the tank, lowering the temperature of the water slightly below that desired, and then heating the water to the temperature required by the thermostatically controlled electric heater.

By means of this equipment it was possible to maintain fairly constant soil temperatures in the containers as well as constant air temperatures within the chambers consisting of the submerged cans. Representative soil-temperature records are compared with the air temperature in the greenhouse in figure 1. Soil-temperature readings, 2 inches below the surface, were recorded several times each day throughout the duration of all the experiments, and in many instances soil-thermograph records were obtained. The mean soil temperature for the duration of the experiments is given in each series of data presented. The Altmann incubator was operated at intervals ranging from about 4° to 30° C. The tanks were operated at regular intervals of 8°, 12°, 16°, 20°, 24°, 28°, 32°, and 36° C., although the mean given in the table in connection therewith may deviate slightly from these temperatures.

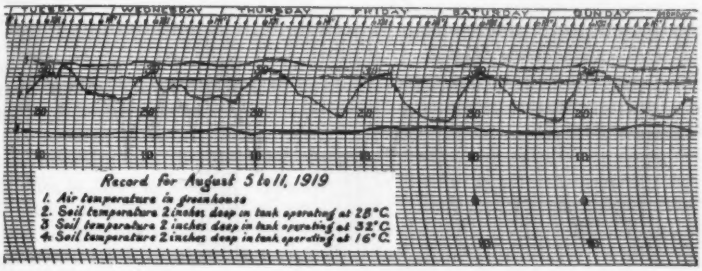

TUESDAY
WEDNESDAY
THURSDAY
FRIDAY
SATURDAY
SUNDAY
Record for August 5 to 11, 1919
1. Air temperature in greenhouse
2. Soil temperature 2 inches deep in tank operating at 28°C.
3. Soil temperature 2 inches deep in tank operating at 32°C.
4. Soil temperature 2 inches deep in tank operating at 16°C.

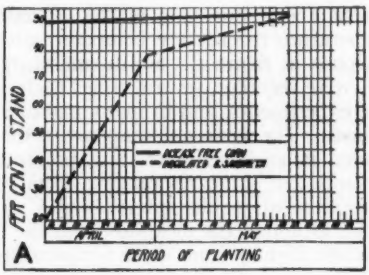
FIG. 1.—Graphic record of greenhouse air temperature and of soil temperature in three different tanks used in the experiments.

The approximate quantity of soil necessary to fill all the cans used in the series was thoroughly screened and mixed, after which the moisture content and moisture-holding capacity of the soil were determined. Sufficient water was then added to bring the moisture up to the desired point of saturation, after which the soil was again thoroughly mixed. After standing covered for a day, the soil was mixed repeatedly and potted, a weighed amount being placed in each can. The cans were equipped with a small inverted flowerpot placed in the soil at about the level of the seed bed. This pot was connected with the surface by a short glass tube fitted with a plug to prevent air circulation. The fully equipped container was then weighed and the weight recorded, after which the can was placed in the temperature tank.

Soil moisture was kept as nearly constant as possible during the progress of the experiments by daily weighing and adding water to restore the original weight. Evaporation from the soil surface was prevented by a dust mulch or coarse sand on the surface. In this way the moisture variation was reduced to a minimum, although it was found impossible to maintain exactly comparable moisture conditions at various soil temperatures. Since the critical range of soil moisture had been previously determined, it seemed logical to believe that the two factors,

moisture and temperature, could be separated and their individual influence studied.

In the field the temperature and moisture experiments were handled by sowing at different dates during the fall and spring. Continuous soil-and-air temperature records were secured by means of the soil-air thermograph, which was checked each day by electrical resistance thermocouples



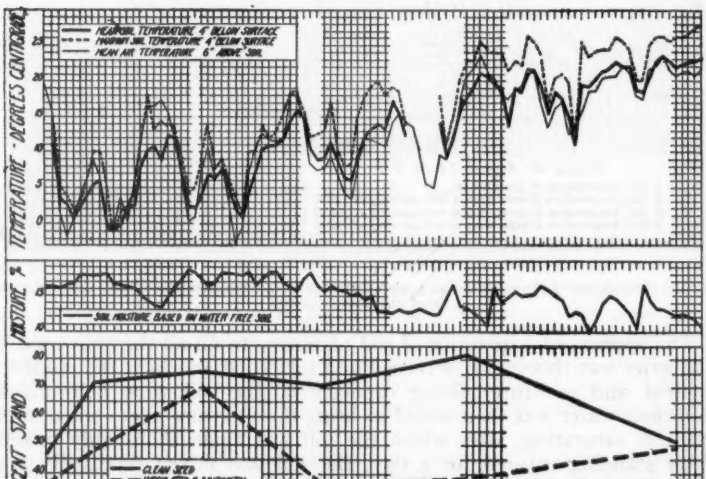


FIG. 2.—Graphs showing soil and air temperature for the season of 1921 and percentage of stand of spring wheat and corn sown on different dates. A, Corn; B, Marquis wheat. The squares of the graph paper are filled in for the seedling period of each sowing, as, for instance, August 24 to 29. This represents the period during which the environmental factors influenced the development of seedling-blight. To avoid confusion the curves for percentage of stand of plants are plotted on the date sown. The distance between the solid lines and broken lines showing stand of check and inoculated plots represents the percentage of seedling-blight.

placed immediately adjacent to the soil-thermograph bulb and left undisturbed for the duration of the experiment. The instrument bulbs were placed in the plots used for the experimental studies at depths of 2 and 4 inches. Sowings were usually made after a rainy period when the moisture content of the soil was at about 15 per cent, based on water-free soil (fig. 2). In some few cases it was necessary to increase the soil-moisture

content by sprinkling the plot the day before planting. Soil-moisture determinations were run before each seeding to insure similar moisture conditions. Thus temperature was the chief soil variant for each seeding, at least during the seedling stage. Of course light intensity and the duration of the light varied for the different seedings, and such factors must be taken into consideration in all work of this type.

INOCULATION TECHNIC

In both wheat and corn the inoculations were made by using a water suspension of conidia of *Gibberella saubinetii*. The conidia were obtained from 3-to-4-day-old cultures. Comparative inoculations with these vegetative conidia and the conidia produced at the end of the vegetative period gave the same type and percentage of blighting. Therefore the vegetative conidia were used, as they could be produced much more rapidly and uniformly.

Sufficient seed for each can of the series was soaked for 10 minutes in the water suspension of the conidia, after which each kernel was lifted out separately with sterile forceps and placed in the sterilized soil in the can. The controls were similarly treated in sterile distilled water.

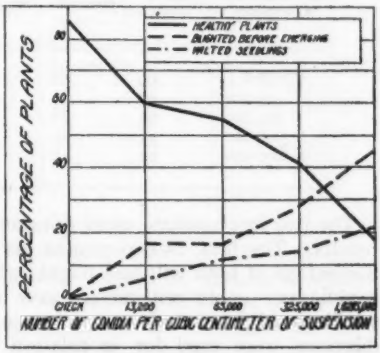


FIG. 3.—Graph showing relation of number of conidia in the inoculum to the development of seedling-blight of wheat. The increased rate of application of conidia in the inoculum on the seed gradually increased both the severity of the blighting and the percentage of plants blighted before emerging.

In several of the early inoculation experiments the number of conidia in the suspension seemed to have a marked influence not only on the percentage of blight produced but also upon the type of blight that resulted. At the outset, therefore, it was necessary to take up a study of this phase of the problem and determine the influence of the number of conidia introduced with the seed on the percentage of blight occurring and the type of blight developing, as well as to determine what spore concentration was most capable of producing a consistent and uniform type of blighting.

The regular temperature cans were prepared, as previously described under the discussion of methods, and filled with soil at 60 per cent of the moisture-holding capacity. The cans were placed in the greenhouse at a temperature of 16° to 20° C. Uniformly plump seed of both Marquis and Turkey wheat was soaked in conidial suspensions ranging from about 13,200 conidia per cubic centimeter to 1,625,000 conidia per cubic centimeter in the most concentrated spore suspension used. These suspensions were prepared by making up a large quantity of a heavy suspension of conidia obtained from vigorous young cultures. The average of a large number of conidial counts made on the haemocytometer was taken as the basis for making the spore dilutions.

With the increase in the number of conidia, there resulted a marked increase in the percentage of diseased plants. Further, with the increase

in the concentration of inoculum, there were gradual increases in both the percentage of seedlings killed preceding emergence and the percentage of those wilted following emergence (Table I and fig. 3). In the more dilute suspensions the attack was usually restricted to the subcrown internode[4] and resulted in a slight blighting, from which in many cases the seedlings recovered. As the number of conidia increased, however, the attack became more general, often including the young plumule, thus resulting in the higher percentages of seedlings which blighted before emergence. A combination of a heavy conidial suspension, together with conditions favorable for the development of the blight, usually resulted in high percentages of the seedlings being killed before emerging (Pl. 5, A).

TABLE I.—*Relation of number of conidia to the production of seedling-blight of wheat and to the type of blight produced*

Average number conidia per cubic centimeter of inoculum.	Percentage germination of wheat.	Percentage of plants emerged.	Percentage of disease-free plants.	Percentage of blighted plants.		
				Slightly diseased.	Wilted.	Blighted before emerging.
Control	99	98	85	13	0	1
13,200	97	80	60	13	7	17
65,000	99	78	56	9	13	21
325,000	93	65	43	7	15	28
1,625,000	90	45	18	6	21	45

The two intermediate spore dilutions seemed to give the most uniform results. The first, 65,000 conidia per cubic centimeter, gave a medium percentage of both wilt and blight, whereas the second dilution, 325,000 conidia per cubic centimeter, gave a relatively higher percentage of seedlings blighted before emergence. Consequently these two spore dilutions were used for inoculation purposes in the soil-temperature and soil-moisture experiments reported in this paper.

TEMPERATURE AND MOISTURE EXPERIMENTS IN THE GREENHOUSE

INFLUENCE OF TEMPERATURE ON THE PARASITE[5]

A considerable literature has been accumulated on the influence of temperature, moisture, and other environing conditions on the development of both saprophytic and parasitic species of the genus Fusarium. Schnaffnit (*25*), Humphrey (*18*), Gilman (*11*), Tisdale (*30*), and others have found that, in general, these organisms develop best at comparatively high temperatures. Their results, however, show that while this group of fungi have fairly high optima, yet they have a very wide temperature range, spore germination, vegetative development, and spore production taking place at a range of from 5° to 36° C.

[4] The designation "subcrown internode," as used for wheat in this paper, applies to the structure between the base of the coleoptile and the crown node.

[5] From unpublished data of experiments conducted by Helen Johann, Grace O. Wineland, and the writer in the Office of Cereal Investigations, Bureau of Plant Industry, United States Department of Agriculture.

SPORE GERMINATION

Conidia from several different strains of *Gibberella saubinetii* were germinated in the Altmann incubator and temperature chambers referred to under methods, at temperatures ranging from 4° to 36° C., in hanging drop cultures of distilled water, soil decoction, and potato-dextrose agar, as well as on poured plates of potato-dextrose agar, and on young wheat seedlings growing in sterile, moist soil. The influence of temperature on rate and percentage of spore germination is shown for one medium, distilled water, in Table II.

TABLE II.—*Influence of temperature on the germination of conidia of Gibberella saubinetii in hanging drops of distilled water*

Mean temperature.	Average germination and length of germ tube.							
	6 hours.		24 hours.		48 hours.		96 hours.	
	Germination.	Length.	Germination.	Length.	Germination.	Length.	Germination.	Length.
°C.	*Per cent*	μ	*Per cent.*	μ	*Per cent.*	μ	*Per cent.*	μ
3.6	0	0	0	0	0.5	0	88	45
11.0	0	0	80	75	86.5	100	.....	.....
17.0	94	100	.....	.....	.....	.....	.....	.....
28.5	97	100	.....	.....	.....	.....	.....	.....
35.0	84	40	.....	.....	.....	.....	.....	.....

The results show that germination and growth take place over a wide temperature range. The cardinal temperatures for germination and growth of the germ tubes were not greatly altered by the use of other media than those given in Table II. The inhibiting influence of the extreme temperatures, however, was more marked in unacidified media. The optimum temperature for both rate and percentage of germination was raised about 4°C. by acidifying the potato-dextrose agar with one drop of 25 per cent lactic acid in each tube of agar. Good germination was obtained from 4° to 32°, but above this temperature the conidia became very much swollen, with much thickened walls and twisted, abnormal germ tubes.

The temperature range for ascospore germination was found to be essentially the same as that for the conidia.

VEGETATIVE DEVELOPMENT

Potato-dextrose agar, both acidified and unacidified, was poured into Petri dishes, care being taken to have dishes of the same size and the same quantity of agar in each plate. A dilute conidial suspension was prepared, and a single loopful was placed in the center of each plate for the series started from conidia. Disks of equal size were cut from the outer circumference of a young colony on agar and placed in the center of the plates for the series started from mycelium. These plates were then incubated in a saturated atmosphere in the temperature chambers previously described under methods, at temperatures ranging from 8° to 36°C. and in the Altman incubator at temperatures ranging from 4° to 30°. The rate of growth was determined by measuring the diameter

of the resulting colonies from day to day. The best comparative data were obtained when the cultures were 4 to 6 days old.

A sparse, slow growth occurred at 3° to 4° C., a light growth developed at 5°, and an appreciable amount of mycelium developed at 8° after an interval of 10 to 12 days. Above this temperature, the rate of growth increased rapidly, the optimum falling at 24° with unacidified agar, and at 28° with acidified agar. Little or no growth occurred above 32° to 34°, regardless of the time incubated. The average diameters of the colonies are given in Table III and shown graphically in figure 4. The diameter and texture of the colonies of a single series are shown in Plate 3, C.

TABLE III.—*Influence of temperature on the vegetative development of Gibberella saubinetii incubated on potato-dextrose agar*

Reaction of medium and inoculum.	Average number determined.	Age of culture (days).	Average diameter of colonies in centimeters at different temperatures.							
			8° C.	12° C.	16° C.	20° C.	24° C.	28° C.	32° C.	36° C.
Unacidified agar, conidia.	8	4	0.1	1.3	2.5	5.9	8.1	7.5	0.3	0
Acidified agar, conidia.	8	4	0	.7	1.7	3.0	3.1	5.7	.1	0
Unacidified agar, mycelium	8	4	1.5	2.5	4.5	6.5	9.0	7.3	1.6	.1
Acidified agar, mycelium.	9	4	.7	1.4	2.3	2.7	4.5	6.0	1.3	0

The cardinal temperatures for mycelial growth were about the same when the fungus was incubated on the stems of young wheat seedlings growing in tubes of sterile soil, the optimum rate of growth ranging from 24° to 28° C. No mycelium was found on the seedlings at temperatures above 32° to 34° C.

PRODUCTION OF CONIDIA

Observations on the production of conidia by the fungus were made on potato-dextrose agar poured plates, in hanging drops of potato-dextrose agar, and on the stems of young wheat seedlings growing in tubes of sterile soil. Conidia were produced at temperatures ranging from 4° to 34° C., as shown in Table IV.

TABLE IV.—*Influence of temperature on the production of conidia by Gibberella saubinetii in hanging drops of potato-dextrose agar*

Time incubated.	Rate of production and comparative number of conidia produced at different temperatures.							
	4° C.	11° C.	17° C.	24° C.	28° C.	30° C.	32° C.	34° C.
24 hours	0	0	0	1	a 3g	10g	10g	0
2 days	0	0	3	10g	10g	10g	10g	2
3 days	0	0	10g	10g	10g	10g	10g	3
4 days	0	1	10g	10g	10g	10g	10g	4
6 days	0	10	10g	10g	10g	10g	10g	4
9 days	0	10g	.....	.....	.....	.....	.....	.....
18 days	0	.....	.....	.....	.....	.....	.....	.....

a Letter g following a number indicates new conidia germinated after being produced.

The time required for the production of conidia varied from about 20 days at 4° C. to 24 hours at 30° to 32°. Sporodocia-like tufts of conidia were produced at the higher temperatures almost as an outgrowth of the conidium. The higher temperatures stimulate the early production of conidia by *Gibberella saubinetii*, as described by Dickson and Johann (9).

INFLUENCE OF SOIL TEMPERATURE ON THE DEVELOPMENT OF HOSTS

While it is not the purpose of this paper to discuss in detail the influence of temperature on the development of wheat and corn, this being reserved for another paper, yet it is desired to give a brief summary in order to be able to present more clearly the relation of the hosts to the development of the disease. The results obtained have demonstrated that temperature is one of the major environmental factors in the physiology of the cereal crops; and, therefore, a knowledge of these temperature responses is of fundamental importance in explaining predisposition to disease. The experiments likewise have shown that other factors, such as soil moisture and light intensity, greatly influence predisposition to disease. Either of these factors, for instance, under certain conditions, may completely overshadow temperature. The study of environmental factors concerned in the development of the seedling-blight has served to bring out clearly the fact that all the environing conditions are inseparably connected and that the degree of blight is the product of a number of factors, any one of which when varied may start a similar set of reactions within the host or parasite. It seems necessary, therefore, to study the responses set up by these environing factors, not only in the parasite but in the healthy host as well.

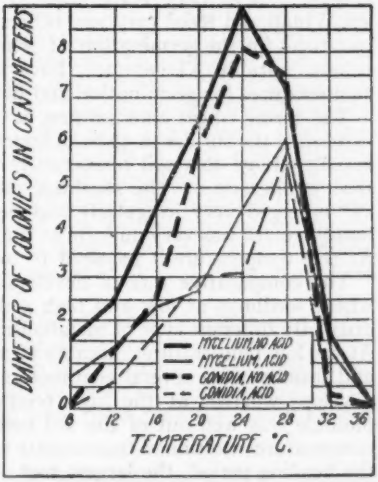


FIG. 4.—Graph showing relation of temperature to the vegetative development of *Gibberella saubinetii* in artificial culture. The optimum temperature for growth, based on maximum diameter of colony, was 24° C. on unacidified agar and 28° on agar acidified with one drop of 25 per cent lactic acid per Petri-dish plate.

INFLUENCE OF SOIL TEMPERATURE ON THE DEVELOPMENT OF MARQUIS WHEAT

Uniform, plump kernels of Marquis wheat were selected for control and inoculated series alike, treated with mercuric-chlorid solution and sown in the soil temperature cans. The soil had been adjusted to the proper moisture content and placed in the cans several days previously. The wheat kernels were planted at a uniform depth of 1.5 inches, after which the cans were covered for 36 hours to prevent excessive evaporation from the soil surface. After uncovering and mulching, the containers were made up to their original weight each day throughout the duration of the

experiments by adding water at the same temperature as the soil. Data were taken on the number of plants emerging, rate of emergence, general appearance, rate of tillering, number of tillers; and in some few instances the plants were grown to maturity and the influence of soil temperature on maturation studied. Upon completion of the experiments the roots were carefully washed free from the soil, after which the length of roots, length of the subcrown internode, height of the plants, and dry weight of roots and tops were determined separately. The data discussed in this chapter are given in condensed form in the seedling-blight discussion. The data indicate that the influence of soil temperature on the cereals tested seems to be greater during the germination period than at any other stage of their development. This is not, however, a new observation, as Gutzeit (*12*) and others have shown this to be true for other plants than the cereals. Sachs (*24*), Haberlandt (*13; 14, p. 39–47, 69–78*), Bialoblocki (*5*), Vinall and Reed (*31*), and others have determined the cardinal temperatures for the germination of wheat, corn, and other cereals. Still others, notably Kincer (*22*), have attempted to correlate the critical temperatures for germination and date of seeding.

The spring wheat emerged first at about 28° C., at which temperature it reached the surface in 38 to 48 hours. The rate of emergence decreased rapidly above this soil temperature—28°—and rather gradually below that temperature. The seedlings produced at soil temperatures above 28° emerged very irregularly and developed unevenly. On the other hand, growth was very uniform at the lower soil temperatures, even at 8°. At this temperature it required 10 to 12 days for the plants to emerge.

The comparative rate of development of roots and plumules of the wheat seedlings at low and high soil temperatures was indicative of a distinctly different type of metabolism at the two temperature extremes. At the low temperatures, notably 8° and 12° C., the roots developed first and usually were several centimeters long before the plumule began to develop; whereas at the high temperatures, notably 28° to 32°, the plumule was well out of the soil before the roots developed. The low temperatures continued to stimulate root development until well towards the heading period, the largest root system for spring wheat developing at about 12° to 16°.

Elongation of the subcrown internode, the first internodal region between the seed and the first node, was greatly stimulated by high soil temperatures. At 24° C. and above, the secondary roots developed at or near the soil surface, while at 8° subcrown internode elongation was almost entirely inhibited, the first node and secondary roots developing immediately above the seed. This inhibition of the subcrown internode at low temperatures persisted even when the seeds were sown at considerable depths below the surface. At temperatures of 16° or above, however, deep seeding or a moist dark compartment greatly increased the length of this region, bringing the secondary roots near the surface of the soil. The response of these tissues to environing factors has been described by Schroeder (*26*), Vogt (*32*), Halsted and Waksman (*15*), and others.

Elongation of the coleoptile, on the other hand, was inhibited by high soil temperatures. At temperatures above 20° C., the growing point of the culm always broke through the coleoptile before emerging from the soil. At temperatures below 16°, however, the coleoptile elongated very much faster than the growing point of the culm and as a result inclosed the growing culm until after emergence, thus preventing the young

growing tip from contact with the soil or soil-inhabiting organisms. At 8°, for instance, the coleoptile usually was 2 to 4 cm. above the surface of the soil before the first leaf pushed through. This variation in type of emergence may help explain the protective influences of low soil temperatures against certain diseases of the small grains.

The largest top production during the early seedling stage was at 20° to 24° C. As the plant increased in age there was a gradual lowering of the optimum temperature for development of tops, until in the later stages of development the best top development resulted at 12° to 16°.

The rate and extent of tillering of spring wheat was modified at the extremes of soil temperature, both high and low. The plants tillered first at the temperatures producing most rapid emergence, namely 24° to 28° C., which indicated somewhat similar cardinal temperatures at this stage of development. Only a limited number of tillers formed at 32° and above. Below this, soil temperature had little effect on tillering until at 8°, where the tillering was limited to two or three culms per plant. The maturation of the wheat plant was hastened by low soil temperatures. Hutcheson and Quantz (*19*) and Appel and Gassner (*2*) have shown this to be true for several of the small grains. The plants grown continuously at a soil temperature of 16° were the first to head and mature. The time of maturation increased slightly with variation in each direction, the plants at 8° maturing at approximately the same time as those at 24°. At temperatures of 24° and above, the heading was retarded very considerably, internodal elongation was reduced, and leaf production stimulated, the spring-wheat plants at 28° heading when only 10 to 12 inches high. Heading was almost entirely inhibited at 32° and above, regardless of the season of the year.

While spring wheat germinated more rapidly at soil temperatures of 24° to 28° C., the germination was more uniform and stronger plants resulted at the lower temperatures—about 8° to 16°. The greatest development of roots as well as of tops occurred at the lower soil temperatures. The earliest maturing, most stocky, and best filled plants resulted at soil temperatures of about 16°.

INFLUENCE OF SOIL TEMPERATURE ON THE DEVELOPMENT OF TURKEY WHEAT

The cardinal temperatures for the development of Turkey winter wheat were, in general, about 4° C. below those for spring wheat. The responses were very similar, except that winter wheat tillered excessively at soil temperatures of 24° and above, and maturation was inhibited by this and higher soil temperatures. Plants grown continuously at soil temperatures of 28° and above were not only checked in their internodal elongation, but failed to form even the embryonic floral organs, the leafy vegetative development continuing throughout the season. Chemical analyses showed this to be a carbohydrate nitrogen balance similar to that described by Kraus and Kraybill (*23*) in the tomato. The analytical data will be discussed in detail in a later paper.

INFLUENCE OF SOIL TEMPERATURE ON THE DEVELOPMENT OF CORN

Disease-free, uniformly matured corn was selected for all the temperature experiments. Usually the seed for the entire series of experiments was taken from a single ear. The corn was planted 1.5 inches

deep after the cans had been prepared as previously described for the wheat series.

Corn emerged first at the soil temperature of 32° C. The rate of emergence decreased gradually below this temperature to 24°. Below this it decreased relatively rapidly to 12°, where emergence occurred in about 14 to 16 days. These results correspond very well with those given for corn by Sachs (*24*), Haberlandt (*13; 14, p. 39–47, 69–78*), Halstead and Waksman (*15*), Vinall and Reed (*31*), and others. At a soil temperature of 8°, although germination occurred, the growth processes were slowed up to such an extent that the plumule rarely reached the surface. At the end of two or three months' time, at this low temperature, the roots elongated 10 to 12 cm. and the plumule had grown several centimeters when the reserves were exhausted and the plant succumbed to the attack of various soil organisms. Only occasionally at 8° did a few plants emerge and become green. The uniformity of emergence and stand decreased rapidly below 20°.

The seedlings produced at the low soil temperatures were stocky, very succulent, and brittle. The leaves were dark green at soil temperatures from 24° to 16° C. Below this the intensity of green decreased until at 12° the leaves were distinctly chlorotic.

The influence of soil temperature on the comparative development of the root and plumule of the corn seedling was similar to that in the wheat seedling, although not so marked. Root development was stimulated at the lower soil temperatures and plumule development inhibited, especially the growing tip, the coleoptile elongating much more rapidly than the shoot. As in wheat, the first leaf did not rupture the coleoptile at the low temperatures until entirely out of the ground.

The largest root system, irrespective of the age of the plant, developed at soil temperatures of about 20° C. The heaviest, as well as the longest, tops developed at about 24° during the earlier period of growth and at about 28° in the later stages of development.

Corn, unlike wheat, matured faster at the higher temperatures, the floral parts developing first at about 32° to 28° C. It has not been possible, due to the retarded vegetative development, to mature corn in the tanks at soil temperatures below 16°.

In general, then, corn functioned at much higher soil temperatures than wheat, the optimum for emergence was 32° C., and the largest, most uniform seedlings resulted at 24° to 28°.

These results indicate that seedlings of spring and winter wheat and corn develop most vigorously and most uniformly at the following soil temperatures: Spring wheat, 16° to 20° C.; winter wheat, 12° to 16°; and corn 24° to 28°.

INFLUENCE OF SOIL TEMPERATURE ON THE DEVELOPMENT OF SEEDLING-BLIGHT IN MARQUIS WHEAT

Studies on the influence of temperature on the development of the parasite have shown that germination of the conidia and vegetative growth take place over a wide temperature range from below 8° to about 32° C. Accordingly a set of experiments was started to determine the range and optimum temperature for infection of wheat seedlings.

Uniform disease-free kernels were treated with mercuric chlorid and after washing thoroughly were soaked in a water suspension of conidia of *Gibberella saubinetii* for 10 minutes, lifted out with sterile forceps,

and placed in the sterilized soil in the cans. All series except two were inoculated with a spore suspension of 65,000 conidia per cubic centimeter. Two series were given a heavier inoculation with 325,000 conidia per cubic centimeter. General growth data were taken on the inoculated and control plants of each series. In addition, daily notes were taken on the number of seedlings showing slight blighting and wilting, and finally upon the completion of the experiments the soil was carefully washed on a screen and each kernel examined for evidence of germination. The columns in Tables V to VII headed "average percentage of germination" represent the total number of kernels which had germinated. The percentage of kernels germinating, the percentage emerging, the percentage of disease-free seedlings, and the percentage of blighted kernels were recorded for each series. The data presented in Table V represent an average of eight different experiments. The results from each were uniform enough to warrant taking an average and explaining the few variations in the discussion of results.

TABLE V.—*Influence of soil temperature on the development of seedling-blight in Marquis wheat*

[Average of eight experiments.]

Average soil temperature.	Average number of days to emerge.	Control.		Inoculated with *Gibberella saubinetii*.		
		Average of percentage germination.	Average percentage of healthy plants.	Average percentage of germination.	Average percentage of healthy plants.	Average percentage of blighted plants.
°C.						
8	16	80	80	84	84	0
12	10	80	80	78	61	17
16	7	79	77	70	48	22
20	7	81	79	75	41	34
24	6	75	71	68	49	19
28	4	74	68	65	43	22
32	4	77	71	73	54	19
36	6	41	16	51	38	13

The influence of soil temperature on the parasite and the hosts has been discussed in detail earlier in the paper. The general rate of development of the seedling, that is, the rate of emergence and rate of tillering and maturing, was not greatly altered by the presence of the parasite. The number of plants emerging, the general appearance of the plants, the length of roots, and the height of plants as well as the weight of both roots and tops, however, were greatly modified by the presence of the parasite.

The germination of spring wheat inoculated with conidia of *Gibberella saubinetii* was reduced by soil temperatures between 12° and 28° C. At a soil temperature of 8°, however, the germination was equal to that of the controls in every series grown. At 12° the germination was reduced, on the average, only 2 per cent (Table V and fig. 5), while at soil temperatures of 16° to 28° the germination was lowered about 8 per cent in each case. The growth of the parasite apparently was sufficiently rapid to penetrate and kill a number of the embryos before they had increased greatly in size, thus reducing germination very

materially within this temperature range. At 32° and above the reduction in germination of the inoculated series was less, in many of the series the percentage germination being as high as that in the controls.

At these higher temperatures, 32° and 36° C., the germination of both controls and inoculated seed was reduced by what was apparently Trichoderma, Penicillium, and other soil organisms attacking the endosperm. The germination of the wheat or corn was not indicative of the extent of damage done by the organism, since many of the kernels germinated and were blighted afterward.

The emergence of the seedlings, therefore, was a better indication of early blighting, although in many cases, especially at soil temperatures of 16° and 20° C., 25 per cent of the seedlings blighted after emerging. The final index, therefore, was the percentage of disease-free and blighted plants at the close of the seedling stage, or about the fourth-leaf stage. Ater this period little, if any, blighting occurred.

The seedling-blight of spring wheat did not occur at soil temperatures of 8° C. or below unless moisture and other environing factors were varied outside of their critical range. At 12°, which was about the critical soil temperature for the production of seedling-blight, both in the tanks and in the field, series grown with a low light intensity blighted badly, whereas series grown in good light showed only a relatively medium degree of blight. In two series of Marquis wheat the temperatures were set at 10° instead of 12°, with the result that seedling-blight was reduced 75 per cent below that at a soil temperature of 12°. The blight was most severe at soil temperatures of 16° to 24°. At this range the seedlings were blighted before emerging and also showed yellowing and wilting during the first-leaf and second-leaf stages. At the higher temperatures, 28° and higher, the blighting usually occurred after the seedlings had emerged. At these temperatures also, as previously stated, the reduction in germination by the parasite became less marked. The maximum rate of emergence of the seedling occurred at about this same temperature range. In all probability, therefore, the seedling developed so rapidly at these temperatures that infection did not take place until after emergence (Pl. 5, C).

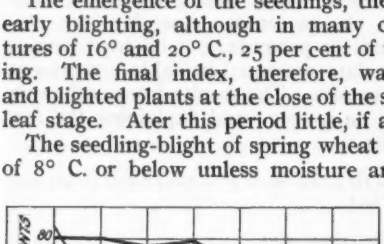


FIG. 5.—Graph showing relation of soil temperature to the development of seedling-blight of Marquis wheat. Average of eight experiments. The distance between the heavy and light lines shows the percentage of seedling-blight. The wheat seedlings blighted at temperatures from about 12° to about 34° C.

The average dry weight per plant, of roots and of tops, was the same in the inoculated and uninoculated series at the soil temperature of 8° C. At soil temperatures of 16° to 28° the weight of both roots and tops in the inoculated series decreased several per cent below that in the controls, which indicated the action of the parasite on the roots of the remaining plants even though blighting did not occur.

At the higher temperatures, 32° to 36° C., there was considerable reduction in the germination and some blighting in both control and inoculated series, especially when grown in nondisinfected soil. Isolations from such seedlings gave some *Gibberella saubinetii* at 32° but

none at 36°. The preponderance of platings gave what was apparently Trichoderma, Penicillium, Rhizopus, and Aspergillus in the order named. These organisms generally invaded the endosperm and developed from there into the seedling.

At other soil temperatures, 12° to 28° C., *Gibberella saubinetii* was universally reisolated, generally in pure culture even in unsterilized soil, if the seedlings were plated before they were badly decomposed. At soil temperatures of 20° to 28° perithecia were often formed in gregarious masses on the first-leaf sheath of the blighted seedlings near the surface of the soil.

Infection takes place and the blight progresses, then, at or above 12° C., but it is rather evident that, for very severe development of the blight, a soil temperature above 16° and below 28° is necessary. Since the attack of the organism is chiefly on the young seedling, the range of temperature during the "nursing period" is undoubtedly the important factor in determining the severity of this stage of the disease.

INFLUENCE OF SOIL TEMPERATURE ON THE DEVELOPMENT OF SEEDLING-BLIGHT IN TURKEY WHEAT

The seven different series of Turkey wheat were handled as previously described for Marquis wheat experiments, except that all of the winter wheat was grown in the fall or early winter. All the series were inoculated with the more dilute conidial suspension, containing 65,000 conidia per cubic centimeter of solution. Data similar to those obtained for Marquis wheat were obtained in all cases. The average results of the seven experiments are given in Table VI and shown graphically in Figure 6.

TABLE VI.—*Influence of soil temperature on the development of seedling-blight in Turkey wheat*

[Average of seven experiments.]

Average soil temperature.	Average number of days to emerge.	Control.		Inoculated with *Gibberella saubinetii*.		
		Average percentage of germination.	Average percentage of healthy plants.	Average percentage of germination.	Average percentage of healthy plants.	Average percentage of blighted plants.
°C.						
8	18	98.0	97.0	96.0	96.0	0
12	12	89.4	89.4	73.1	67.1	6.0
16	8	95.5	95.5	60.1	47.3	12.8
20	6	96.5	93.0	61.7	44.7	17.0
24	5	82.5	82.5	67.6	49.3	18.3
28	4	80.4	77.7	56.1	35.0	21.1
31	6	62.5	62.5	59.2	57.1	2.1
35	10	48.0	43.7	25.9	25.9	0

The response of winter wheat to the blight was similar, in almost all cases, with that described for spring wheat in the previous pages. The only differences noticeable were that blighting was more severe at 20° in the Marquis series and was less extensive in the winter wheat seedlings at a soil temperature of 12° C. The average percentage of blighted seedlings in the winter wheat was less at all temperatures, but

as all of these series were inoculated with the suspension of 325,000 conidia per cubic centimeter, these differences can be partially explained. There was, however, some evidence that Turkey wheat was less susceptible to the blight than the Marquis wheat. More experiments are necessary with these two wheat varieties to confirm these results.

In comparing the influence of temperature on the parasite in pure culture and on the production of the blight of wheat seedlings, the temperature influence at first thought seems rather simple. It appears that wheat is capable of growing at soil temperatures lower than those at which the parasite can develop and become parasitic. The wheat plant, therefore, escapes the disease, the blight occurring only at temperatures which stimulate the growth of the parasite. Such a relationship was pointed out by Clayton[6] in the tomato-wilt caused by *Fusarium lycopersici* Sacc., where the wilt curve produced in response to soil temperature coincides with the growth curve of the organism in pure culture, the optimum for both occurring at about 28° C. Upon closer analysis, however, the relationship seems far more complex and distinctly different from that existing in the tomato-wilt problem.

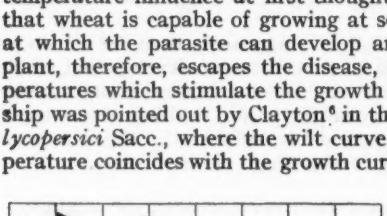


FIG. 6.—Graph showing relation of soil temperature to the development of seedling-blight of Turkey wheat. Average of seven experiments. The distance between the heavy and light lines shows the percentage in seedling-blight. Compare with spring wheat of figure 5.

The parasite has an extremely wide temperature range for both spore germination and growth, and furthermore, while a histological study of the wheat seedlings at the low temperatures demonstrated an abundance of the mycelium of the parasite around the subterranean portions of the seedlings, yet no penetration could be detected. The hyphae were twisted around the root hairs and matted on the cortex of the roots and coleoptile. In many places swollen tips of the hyphae were pressed tightly into the intercellular spaces on the epidermis of the coleoptile and against the root hairs, yet were seemingly unable to penetrate between the cells or gain entrance through the membrane of the root hairs, whereas at the high temperatures the hyphae readily penetrated any of the young seedling tissues, gaining entrance through the root hairs as well as through the epidermal cells of the coleoptile, subcrown internode, and roots.

These studies, then, seemed to indicate a relationship at least between host and parasite almost the reverse of that in the tomato-wilt. The influence of environment upon the host appeared to be the fundamental cause of the response. The wheat seedling seemingly was unable to react favorably to the higher soil temperatures and thus succumbed to the blight. The results have shown that a short exposure to high temperatures during the germination period unbalanced the wheat seedling and thus made it susceptible to the parasite.

[6] From unpublished data of studies conducted in the Department of Plant Pathology, University of Wisconsin.

INFLUENCE OF SOIL TEMPERATURE ON THE DEVELOPMENT OF SEEDLING-BLIGHT IN CORN

The experiments on the relation of soil temperature to the seedling-blight of wheat have shown that blight does not occur much below 12°C., and that at 12° and above the wheat seedling becomes susceptible to attack. The investigations seem to demonstrate further that the response of the host to soil temperature rather than that of the parasite must be considered as the chief explanation of these differences. Accordingly, another series of experiments was started with a different host, namely, corn, which is a comparatively warm-climate crop and is susceptible to the same parasite, *Gibberella saubinetii*.

The seed for each series of experiments was taken from the same ear of corn. The method of inoculation and planting was identical with that previously described for wheat. Observations comparable to those recorded for wheat were made; in fact, in all but two series wheat was grown simultaneously with corn in the same temperature tanks. The data given in Table VII and shown graphically in figure 7 represent the average of seven different series of corn experiments.

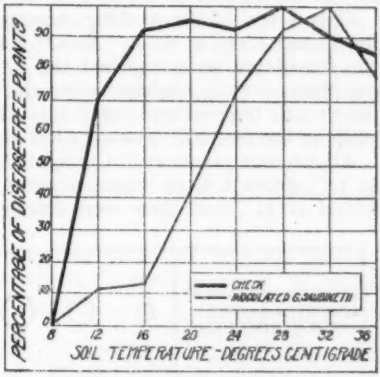


FIG. 7.—Graph showing relation of soil temperature to the development of seedling-blight of corn. The distance between the heavy and light lines shows the percentage of seedling-blight. Compare with seedling-blight of wheat in figures 5 and 6.

TABLE VII.—*Influence of soil temperature on the development of seedling-blight of corn*

[Average of seven experiments.]

Average soil temperature °C.	Average number of days to emerge.	Control.		Inoculated with *Gibberella saubinetii*		
		Average of percentage germination.	Average percentage of healthy plants.	Average percentage of germination.	Average percentage of healthy plants.	Average percentage of blighted or diseased plants.
8	.....	50	.....	0	0	0
12	15.7	77	72	20	11	9
16	9.7	96	92	54	12	42
20	5.7	97	95	89	42	47
24	5.0	92	92	100	73	27
28	3.6	100	100	94	93	1
32	3.0	97	90	100	100	.....
36	3.6	98	85	97	77	[a] 20

[a] No blighting; killed chiefly by high soil temperatures.

The rate of development, at least during the seedling stage, was checked slightly by the introduction of the parasite at soil temperatures below 24° C., but above this no differences were detected.

The germination of the corn inoculated with conidia of *Gibberella saubinetii* was influenced by soil temperatures between 8° and 20° C. At a soil temperature of 8° the embryos of all the kernels were invaded and killed before germination. Germination was reduced an average of 57 per cent below the controls at 12° and 42 per cent at 16°. At 20° the reduction in germination was strikingly less, only 8 per cent, and at 24° all the kernels germinated in the seven series grown.

Only a few of the seedlings emerged in the controls and none in the inoculated series at 8° C. At 12° about 50 per cent of the seedlings in the inoculated series reached the surface before blighting, the remaining plants usually blighting when the plumule was from 1 to 3 cm. long. Above this temperature practically all the seedlings emerged and wilted while in the first-leaf or second-leaf stage (Pl. 4).

All the corn plants at 8° C. blighted; all but about 12 per cent blighted at 12°; about half of them blighted after wilting at 20°; only a few wilted at 24°, and these were chiefly in two series of a very suscept-

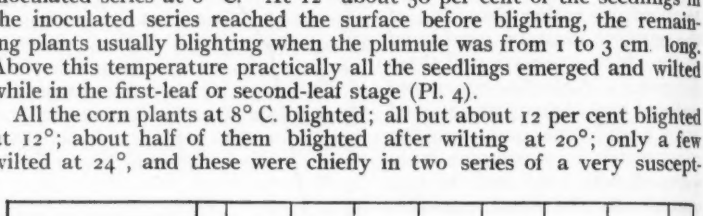


FIG. 8.—Graph showing relation of soil temperature to the vegetative development of the parasite and the production of the disease. A graphic summary of the vegetative development of *Gibberella saubinetii* in artificial culture and the comparative quantities of seedling-blight of corn and wheat at different soil temperatures. The black portion of the circle shows the average percentage of blighted seedlings.

ible strain of Ninety-Day corn. Many of the plants showed root lesions and some were weakened by the root attack but usually were capable of recovering and later making a medium growth, especially if put at the higher temperatures. A few plants at 28°, in the two series previously mentioned, showed small root lesions but none sufficient to hinder the development of the plant. The blight was most severe at 8° to 16°, where only a few plants survived, and stopped abruptly at 24°. At this temperature root lesions occurred in a few cases but in most of the series did little damage to the plants.

The average dry weight per plant of roots and tops of the so-called disease-free plants in the inoculated series at temperatures from 12° to 24° C., was much below that of the control plants; above this temperature the weights were approximately the same.

The parasite was isolated in pure culture from the seedlings, the endosperms, and the roots of the blighted and diseased seedlings. After remaining in the soil a week or two there was a development of sapro-

phytes, especially bacteria, which often crowded out *Gibberella saubinetii* entirely.

In corn, infection takes place and blight progresses, then, at all temperatures below 24° C. The most rapid development of the disease and the maximum blighting occur at 12° and 16°. Below this, namely, at 8°, where wheat is entirely resistant to the attack of this parasite, corn succumbs entirely (fig. 8 and Pl. 4 and 5).

As the temperature range for the production of blight in this warm-climate plant is the reverse of that for wheat, a cool-temperature plant, it is only logical to say that this parasite is capable of attacking both hosts during their seedling stages when they are subjected to unfavorable environmental conditions. This fact is brought out even more strikingly in the following combined moisture and temperature studies.

INFLUENCE OF SOIL MOISTURE ON THE DEVELOPMENT OF SEEDLING-BLIGHT IN WHEAT

Earlier studies conducted in connection with this problem demonstrated that the influence of moisture on the seedling-blight of wheat was similar to that of temperature,[7] for low soil moistures increased the susceptibility of the wheat seedling and thus increased the virulence of the attack. The influence of soil moisture gradually decreased until at 45 to 50 per cent of the moisture-holding capacity of the soil this factor ceased to influence blighting. As a consequence all the temperature experiments were conducted with a soil at 60 per cent of the moisture-holding capacity, assuming that in this way moisture could be separated from temperature and the critical range of the latter be determined.

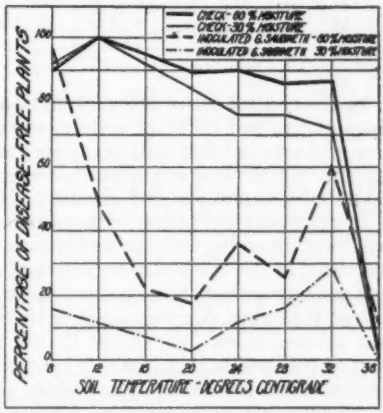


FIG. 9.—Graph showing relation of soil temperature and moisture to the development of seedling-blight of wheat. Compare the solid lines with the broken lines. Note the abundant blighting at 8° C. in the soil with a moisture content of 30 per cent of the moisture-holding capacity.

In order to study further the influence of moisture on the host and parasite two different temperature series of plants were grown at three different soil-moisture contents, 30, 45, and 60 per cent of moisture-holding capacity. The cans of soil at different moisture contents were prepared, inoculated, and sown as described in the previous experiments. The seed was inoculated with the heavy conidial suspension, 325,000 conidia per cubic centimeter, in order to get the maximum temperature and moisture response. The average percentage results of the two series are given in Table 8 and figure 9.

[7] Credit is gladly given to Mr. B. Koehler for conducting the earlier studies on the relation of soil moisture to seedling-blight.

TABLE VIII.—*Influence of soil temperature with varying degrees of soil moisture on the development of seedling-blight of wheat*

[Average of two experiments]

Average soil temperature.	30 per cent moisture-holding capacity.					45 per cent moisture-holding capacity.			60 per cent moisture-holding capacity.				
	Control.		Inoculated.			Inoculated.			Control.		Inoculated.		
	Percentage germinated.	Percentage disease-free.	Percentage germinated.	Percentage disease-free.	Percentage diseased.	Percentage germinated.	Percentage disease-free.	Percentage diseased.	Percentage germinated.	Percentage disease-free.	Percentage germinated.	Percentage disease-free.	Percentage diseased.
°C.													
8	96	96	88	16	72	100	56	44	90	90	96	96	0
12	100	100	96	12	84	80	24	56	100	100	96	48	48
16	100	96	92	8	84	72	20	52	95	95	86	22	64
19	88	84	80	4	76	52	20	32	95	89	88	18	70
23	76	76	72	12	60	96	8	84	95	90	84	36	48
27	92	76	60	16	44	88	24	64	92	86	84	26	58
31	92	72	64	28	36	100	32	68	87	87	96	60	36
35	36	0	64	0	[a] 56	48	12	[a] 12	0	0	44	12	32

[a] Balance killed by high soil temperatures.

In the control series the germination and number of disease-free seedlings at the two different soil-moisture contents, 30 and 60 per cent of the moisture-holding capacity, were the same at the lower temperatures. At the higher temperatures, however, the low soil moisture slightly inhibited germination and plant development.

In the inoculated series, on the other hand, the germination percentage of seedlings emerging and the percentage of blighted seedlings were greatly increased in the low soil moistures and even at the low soil temperatures. Soil moisture, then, became the limiting environmental factor to such an extent that even the resistance in the seedlings at the low temperatures was broken down. At the 8° C. soil temperature, for instance, 72 per cent of the seedlings grown at 30 per cent moisture were blighted, 48 per cent of them before emerging, while 44 per cent of the seedlings grown at 45 per cent moisture were blighted, and 24 per cent of these were blighted before emerging. This was in marked contrast to the results at 60 per cent moisture, where, as in the previous experiments, no blight occurred. The percentage of blighted seedlings was correspondingly increased by low soil moisture at all temperatures (Pl. 5).

Soil moisture, then, was another important factor in predisposing the seedlings to attack by *Gibberella saubinetii*. And when moisture was the limiting factor, it was impossible to obtain the true temperature influences.

TEMPERATURE AND MOISTURE EXPERIMENTS IN THE FIELD

The greenhouse experiments have demonstrated that wheat and corn seedlings become susceptible to the wheat-scab parasite only when under unfavorable environmental conditions, which may be a single factor, such as temperature, moisture, soil reaction, and others, or a combination of several of these factors. These experiments have shown, further, that the two hosts respond conversely to at least one factor,

namely, temperature. That is, wheat blights in a comparatively warm soil above 12° C., whereas, on the other hand, corn blights in a cool soil below 20° to 24°. Inasmuch as certain of these factors, especially temperature and moisture, play an important rôle in forming the field environment for both wheat and corn seedlings, a series of periodic field sowings were made at Madison, Wis., during the spring and fall of 1920 and the spring of 1921. These should point toward possible remedial measures for this and similar seedling diseases of the cereal crops as well as check against the greenhouse results.

A uniform plot of land was prepared for the spring sowings in the previous fall and reworked at the earliest possible date in the spring. It has happened in the past two years that early in March the soil has warmed and dried sufficiently to permit the installation of the thermographs and electrical resistance thermometer bulbs to obtain soil-temperature readings and to sow the first wheat. Following this the temperatures have gone down again during the remainder of March and most of April. It has been possible in this way, by watching the daily soil temperature and moisture, to make seedings at different intervals, especially a few days after a rain when moisture was well within the limits of plant response (fig. 2), which would throw the germination period of the grain at soil temperatures below or above the critical temperatures for seedling-blight. By this method it has been possible to check the constant soil-temperature studies in the greenhouse with fluctuating field temperatures.

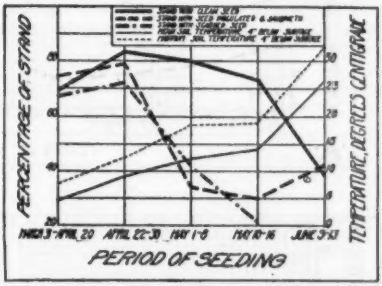
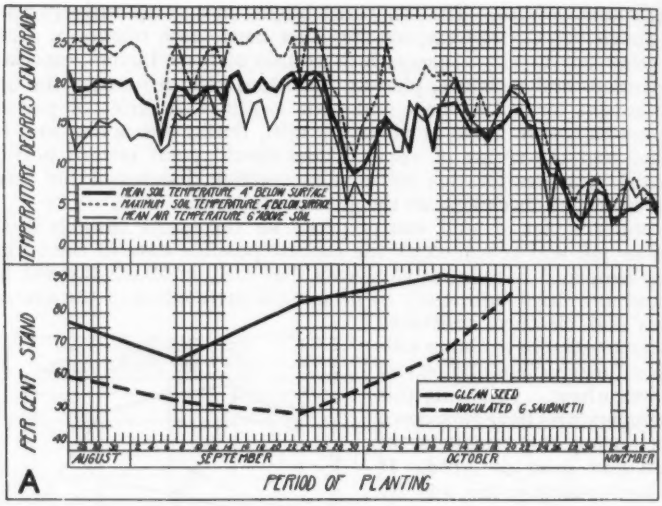


FIG. 10.—Graph showing relation of date of seeding to the development of seedling-blight of Marquis wheat in 1920. No blight occurred in the cool soil during March and April when the mean soil temperature was below 12° C. On the other hand, abundant blight developed in the later seedings, May 1 and 10, until the high soil temperatures of June inhibited the development of the parasite. (Summary of fig. 11.)

RELATION OF DATE OF SEEDING TO THE DEVELOPMENT OF SEEDLING-BLIGHT IN MARQUIS WHEAT

EXPERIMENT IN 1920

Two sowings were made on March 31 and April 22, which germinated before the average mean soil temperature was above 12° C. Following this, two sowings were made on May 1 and 10, which germinated with an average mean soil temperature between 12° and 15°. Finally, a sowing was made on June 9, during a period when the average mean soil temperature was about 26°, and the maximum running up to 36° for several hours during the middle of the day. Each sowing of these different periodic series consisted of 10 rod rows for control and inoculated seed and 5 rod rows for scabbed seed. The duration of the germination period, the percentage stand of disease-free plants, and the average mean temperatures are given in Tables IX and X and shown graphically in figure 10. The mean daily and daily maximum soil temperatures 4 inches below the surface and mean daily air temperatures 6 inches above the soil, together with the percentages of healthy plants in the different seedings, are given in figure 11.



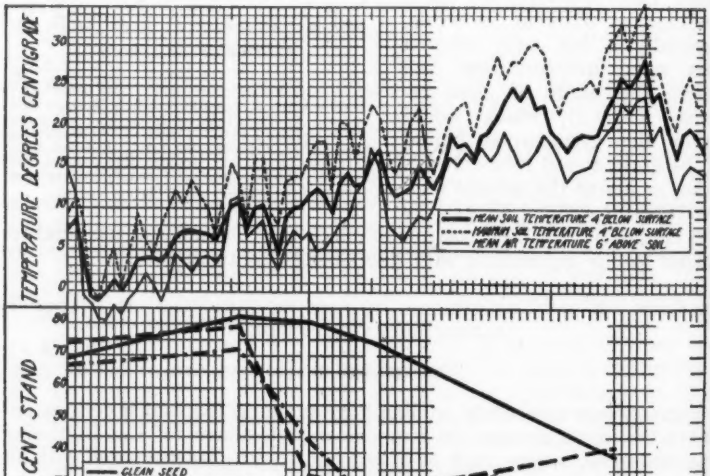


FIG. 11.—Graphs showing soil and air temperatures for the season of 1920 and percentage of stand of spring and winter wheat sown at different dates. A, Fall-sown Turkey wheat; B, spring-sown Marquis wheat. The squares of the graph paper are filled in for the seedling period of each sowing, as, for instance, August 24 to 29. This represents the period during which the enviromental factors influenced the development of seedling-blight. To avoid confusion the curves for percentage of stand of plants are plotted on the date sown. The distance between the solid lines and broken lines showing stand of control and inoculated plots represents the percentage of seeding-blight.

TABLE IX.—*Average soil and air temperatures during germination periods of Marquis wheat at Madison, Wis., in the spring of 1920*

Duration of germination period.		Average soil temperatures, 4 inches deep.			Average air temperatures, 6 inches above soil.		
Dates.	Number of days.	Mean.[a]	Min.	Max.	Mean.[a]	Min.	Max.
		°C.	°C.	°C.	°C.	°C.	°C.
Mar. 31 to Apr. 20	21	4.5	2.3	7.7	1.8	−1.9	6.3
Apr. 22 to 30	9	8.9	6.2	12.5	6.7	3.2	10.7
May 1 to 8	8	12.3	7.4	17.8	7.0	2.0	14.5
May 10 to 16	7	13.9	9.4	18.6	8.9	4.1	14.2
June 9 to 13	5	26.2	20.7	32.3	22.7	17.4	28.1

[a] Mean temperatures in this and succeeding tables were computed by adding together the temperatures recorded at hourly intervals during the germination period and dividing the sum by the number of hours in the period.

TABLE X.—*Relation of date of seeding to the development of seedling-blight of Marquis wheat at Madison, Wis., in the spring of 1920*

Date of seeding.	Average number of days for emergence.	Average percentage stand.		
		Clean seed not inoculated.	Clean seed inoculated with *Gibberella saubinetii*.	Naturally scabbed seed.
Mar. 31	22	69.0	74.2	66.5
Apr. 2	8	82.5	79.1	72.5
May 1	8	80.1	37.5	47.0
May 10	7	74.7	27.5	22.3
June 9	6	38.0	42.0	.....

The stands of healthy plants from the uninoculated, the inoculated, and the scabbed seed were practically the same for the first planting, which required 22 days to germinate—that is, the period from March 31 to April 20. The germination in all seed-lots was lowered by continued freezing and thawing during germination, but no blight appeared in any of the plots. The stand in the second series of seedings was greatly increased, due to more favorable weather during the germination period of 8 days. A limited number of blighted seedlings, however, appeared toward the last of the period in both the inoculated and scabbed series. The percentage of disease-free seedlings in the next two seedings was reduced 43 to 47 per cent, respectively, below the stand in the controls. The average mean temperature during the germination period and the daily temperature curves in figures 10 and 11 show a soil temperature below 12° C. for the first two seedings, and above 12° for the two May seedings. The critical soil temperature for seedling-blight in the field, therefore, corresponds very closely with that in the soil-temperature tanks.

The results from the last seeding, June 9, which was made during the extremely high temperatures, also agreed with the greenhouse results. That is, while germination was greatly reduced in both control and inoculated plots, no seedling-blight appeared, due probably to high temperatures inhibiting the development of the parasite.

The root systems of both the inoculated and control series of plants were excavated and studied at the maturity of the crop. Trenches were dug across the adjoining rows of the inoculated and control series in the March 31 and May 10 plantings, after which a gentle stream of water was used to wash the soil away from the roots. In this way a comparison was obtained, not only of the general root development but also of the root distribution. The development of lateral feeder root branches, the depth of root penetration, and the comparative root development in the two different seedings, as well as the influence of the fungus on reducing the root system, are shown in Plate 6, A, B, and C. The roots penetrated much deeper and developed more lateral branches in the early seedings

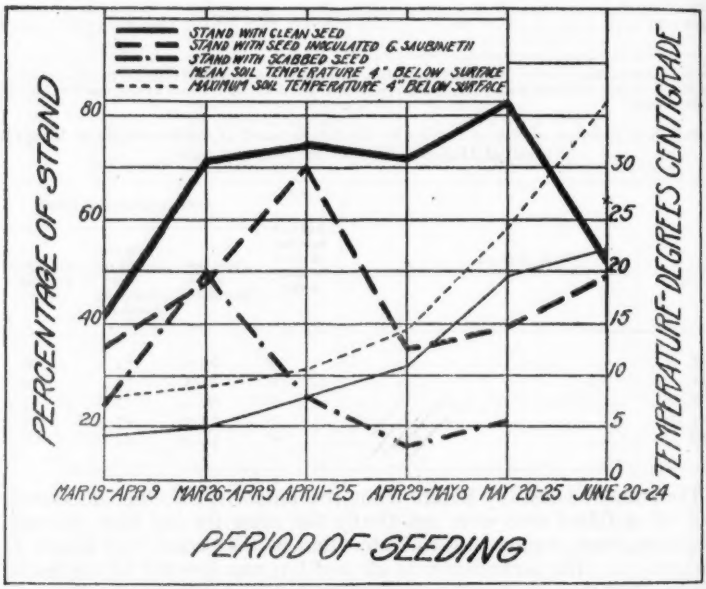


Fig. 12.—Graph showing relation of date of seeding to the development of seedling-blight of Marquis wheat in 1921. Results are essentially the same as in the previous season, shown in figure 10. (Summary of fig. 2.)

which were grown at a low soil temperature. Likewise, the parasite did not reduce the size of the root system at the low temperature, but the roots of the inoculated plants in the later seeding at high soil temperature were reduced nearly 50 per cent below those of the control plants.

EXPERIMENTS IN 1921

Three sowings made on March 19, March 26, and April 11, germinated before the average mean soil temperature for the germination period was above 12° C. The mean daily soil temperature for several days at a time during these three periods, however, was above 12°. The next two seedings, made on April 29 and May 20, germinated at an average mean soil temperature considerably above 12°, whereas the last seeding, on June 20, germinated during a fairly high mean soil temperature and fairly high maximum soil temperature.

The percentage of stand as well as the average mean soil temperature and mean daily soil temperature are given in Tables XI and XII and shown graphically in figures 2 and 12.

TABLE XI.—*Average soil and air temperatures during germination periods of Marquis wheat at Madison, Wis., in the spring of 1921*

Duration of germination period.		Average soil temperatures, 4 inches deep.			Average soil temperatures, 6 inches above soil.		
Dates.	Number of days.	Mean.	Min.	Max.	Mean.	Min.	Max.
		°C.	°C.	°C.	°C.	°C.	°C.
Mar. 19 to Apr. 9	21	4.6	2.8	7.8	7.3	2.4	12.4
Mar. 26 to Apr. 9	14	4.8	3.2	8.4	7.7	2.4	13.3
Apr. 11 to 25	14	7.7	5.4	10.7	8.9	4.8	12.9
Apr. 29 to May 8	9	10.5	6.5	14.7	8.5	3.5	13.5
May 20 to 25	5	19.6	15.4	23.9	20.8	15.4	26.4
June 20 to 24	4	22.5	19.6	26.7	21.0	17.2	27.7

TABLE XII.—*Relation of date of seeding to the development of seedling-blight of Marquis wheat at Madison, Wis., in 1921*

Date of seeding.	Average number of days for emergence.	Average percentage of stand.		
		Clean seed not inoculated.	Clean seed inoculated with *Gibberella saubinetii*.	Naturally scabbed seed.
Mar. 19	21	40.6	35.6	24.0
Mar. 26	14	71.6	47.6	49.6
Apr. 11	14	75.2	70.0	26.4
Apr. 29	9	71.7	35.8	17.8
May 20	5	83.0	39.6	21.2
June 20	4	52.0	49.2	.....

In general, the results in the second spring showed the same temperature responses as those of the previous year. The early seedings gave the highest stand of healthy plants, although some blight appeared in these plots, due probably to the fluctuating soil temperature and moisture. In all three germination periods of the first seedings the mean daily soil temperature was around or above 12° C. for several days at a time. Likewise, especially in the second germination period, the soil moisture was low enough to be an important factor in producing blight. The following two seedings both gave high percentages of blight, or, stating it reversely, a poor stand. The last seeding corresponded with the last seeding of the previous spring, which demonstrated that the attack of the parasite was probably checked by the high soil temperatures.

RELATION OF DATE OF SEEDING TO THE DEVELOPMENT OF SEEDLING-BLIGHT IN TURKEY WHEAT

The first sowings of winter wheat in 1920 were made in August when the soil temperature was fairly high. The fall was unusually warm, however, and the mean soil temperatures did not drop below 12° C. during September and early October, so that it was necessary to continue the seedings late into October to secure the low soil temperatures. All of the plots were sown when the temperature of the soil was above 12° C. except the last plot, sown on October 20. The percentage of stand and soil and air temperatures are given in Tables XIII and XIV and are shown graphically in figures 11 and 13.

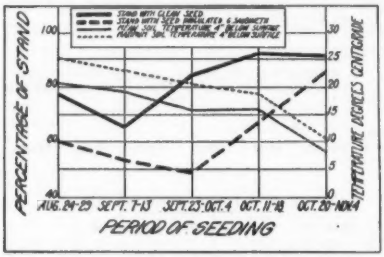


FIG. 13.—Graph showing relation o date of seeding to the development of seedling-blight of Turkey wheat in 1920. The cool soil temperatures of the late fall reversed the curves from those of figures 10 and 12. (Summary of figure 11.)

TABLE XIII.—*Average soil and air temperatures during germination periods of Turkey wheat at Madison, Wis., in the fall of 1920*

Duration of germination period.		Average soil temperatures, 4 inches deep.			Average air temperatures, 6 inches above soil.		
Dates.	Number of days.	Mean.	Min.	Max.	Mean.	Min.	Max.
		°C.	°C.	°C.	°C.	°C.	°C.
Aug. 24 to 29	6	20.4	16.3	25.0	14.4	10.0	21.5
Sept. 7 to 13	7	19.2	15.4	23.5	17.2	11.6	23.1
Sept. 23 to Oct. 4	12	15.8	12.3	20.2	13.9	8.4	20.3
Oct. 4 to 18	9	15.9	14.3	18.7	17.4	13.2	20.8
Oct. 20 to Nov. 4	16	8.2	6.8	11.3	9.5	6.0	13.7

TABLE XIV.—*Relation of date of seeding to the development of seedling-blight and winter-killing of Turkey wheat at Madison, Wis., in the fall of 1920*

Date of seeding.	Average number of days for emergence.	Average percentage of stand, fall, 1920.		Average percentage of stand, spring, 1921.		Average percentage of winter killing.	
		Control.	Inoculated.	Control.	Inoculated.	Control.	Inoculated.
Aug. 24	6	77.0	60.0	68.0	48.8	9.0	11.2
Sept. 7	7	55.0	53.0	44.0	48.2	11.0	4.8
Sept. 23	12	83.5	49.5	56.0	31.6	27.5	17.9
Oct. 9	9	92.0	67.0	49.2	29.2	42.8	37.8
Oct. 20	16	90.0	86.0	71.7	57.8	18.3	28.2

The first two sowings showed the influence of high soil temperature upon both host and parasite. The germination and stand of the controls was greatly reduced, yet the reduction in germination and stand from blight was not as great as in the following two sowings where the mean soil temperature was 16° C. The last seeding, however, in which the seed germinated in a cool soil, gave little blighting, and, further, the stand and general vigor of the plants were comparable to the condition of the controls.

These soil-temperature experiments in the field have shown, then, that wheat germinated in a cool soil resists the blight but when germinated in a warm soil succumbs to the attack. These results also have shown that the critical soil temperature for the production of the seedling-blight of

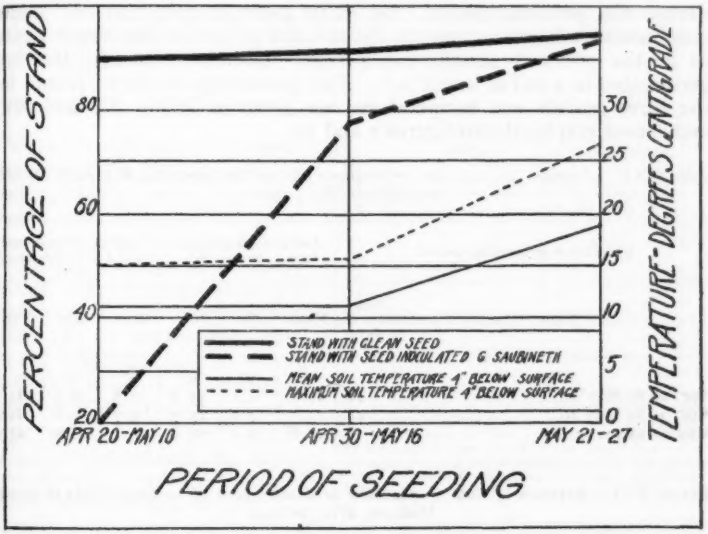


FIG. 14.—Graph showing relation of date of planting to the development of seedling-blight of corn in 1921. The seedling-blight occurred during the April plantings when the mean soil temperature was below 20° C. No blight developed when the mean soil temperature reached 20° C. (Summary of fig. 2.)

wheat is the same under field conditions as in the soil-temperature tanks in the greenhouse, namely, about 12° C.

These results already have been applied as control measures by agronomists and other wheat growers, yet further emphasis is necessary from the phytopathological viewpoint. Seeding at the earliest safe date in the spring for spring wheat and the latest safe date in the fall for winter wheat is the best method of reducing the seedling-blight. Agronomists have shown that the date of planting has a marked relation to lodging and to yield and quality of grain. The marked reaction between the date of seeding and the root development may partly explain those relations.

RELATION OF DATE OF PLANTING TO THE DEVELOPMENT OF SEEDLING-BLIGHT IN CORN

The general field observations during the past two seasons have demonstrated beyond question the influence of soil temperature upon the seedling-blight of corn and, in themselves, have corroborated the soil-temperature studies in tanks in the greenhouse. A preliminary series of periodic planting experiments with corn was started in the spring of 1921 to check more exactly the soil-temperature tank results. The first planting, April 20, germinated when the mean soil temperature was about 12° C.; the second planting, April 30, germinated a few days before most of the corn was planted in the vicinity of Madison. While the average mean soil temperature in this period was about the same as during the previous period, the daily mean temperature, as shown graphically in figures 2 and 14, did not run as low at any single period as in the previous germination period. The last planting, May 31, germinated in a soil at about 20°. The percentage stand of plants for the three periods and temperatures are given in Tables XV and XVI and shown graphically in figures 2 and 14.

TABLE XV.—*Average soil and air temperatures during the germination periods for corn at Madison, Wis., 1921*

Duration of germination period.		Average soil temperatures, 4 inches deep.			Average air temperatures, 6 inches above soil.		
Dates.	Number of days.	Mean.	Min.	Max.	Mean.	Min.	Max.
		°C.	°C.	°C.	°C.	°C.	°C.
Apr. 20 to May 10	20	11.7	8.1	15.2	10.8	6.3	15.5
Apr. 30 to May 16	16	11.7	8.0	15.5	9.7	4.8	14.4
May 21 to 27	6	18.8	15.5	26.8	20.1	15.7	25.2

TABLE XVI.—*Relation of date of planting to development of seedling-blight of corn at Madison, Wis., in 1921*

Date of planting.	Average number of days for emergence.	Average percentage of stand.	
		Disease-free seed.	Disease-free seed inoculated with *Gibberella saubinetii*.
Apr. 20	20	90	20
Apr. 30	16	91	78
May 21	6	94	93

The first planting was most severely affected by blight, 70 per cent of the plants being killed during the seedling stage. Most of these were blighted during germination or just before emergence. The mean daily soil temperature, as shown graphically in figure 2, contributed directly to this blighting. The soil temperature following sowing was

high enough to start immediate germination. This was followed in 8 days by a low temperature period of about 10 days' duration in which the temperature went considerably below the critical temperature for blighting.

The second planting was made during the low-temperature period, but did not begin germinating until the soil temperature had risen to about 16° C. While this planting was subjected to low soil temperatures later in the germination period, the soil temperatures did not go as low as those following the previous planting, and the depression occurred later in the period of seedling development. As a result, the stand was reduced only 13 per cent. The last planting showed only a small degree of blighting in two or three of the most susceptible strains.

The field temperature experiments with corn in general showed results similar to those obtained in the greenhouse. The field plantings, however, indicated a slightly lower critical temperature for blighting than that shown in the soil temperature tanks in the greenhouse.

DISCUSSION OF RESULTS

While the influence of soil temperature in the development of seedling-blight was operative over a wide range of temperatures, there was, however, in both wheat and corn a very clearly defined critical temperature for blighting. Soil temperatures below 12° C., for instance, prevented blighting of the wheat seedlings, whereas soil temperatures at 12° or above produced a large amount of blight. The critical soil temperature, therefore, for the seedling-blight of wheat was always at 12° C., whether a constant soil temperature or the mean of a fluctuating field soil temperature. The critical soil temperature is represented graphically in Figures 5 and 6 for the constant soil temperature series and in Figure 15 for one instance in the field series. Other cases equally striking could be chosen from periodic seedings of either the spring or the winter wheat.

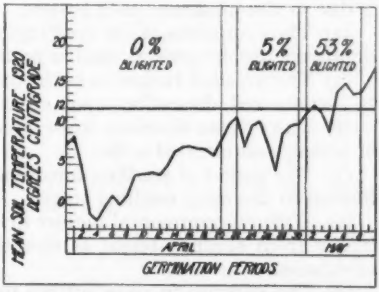


FIG. 15.—Graph showing critical soil temperature for the development of seedling-blight of wheat. The heavy horizontal line at 12° C. represents the critical soil temperature for the development of blight in the soil-temperature tanks in the greenhouse. The rise of the daily mean soil temperature to and above the 12° C. line resulted in the development of seedling-blight.

The straight line at 12° C. in figure 15 represents the approximate critical soil temperature for seedling-blight of wheat. The first seeding germinated and emerged when the soil temperature curve was well below this line, with no blight as a result. The second sowing developed in a warmer soil with a mean temperature still below the 12° line, yet approaching it. In many cases the temperature during a portion of the day was above this line. The blight appeared on just a few of the seedlings. The last seedings shown developed in a soil having a mean temperature of 12° or above, and as a result 53 per cent of the plants were blighted. The mean soil temperature in fluctuating field temperatures corresponded very closely with the constant soil temperatures in the greenhouse experiments.

The seedling-blight of corn, both in greenhouse tank series and in field series, developed at 20° to 24° C. and below, while above 24° no

blight occurred. The critical soil temperature for the development of of seedling-blight of corn, therefore, is about 20° (fig. 7). Here, again, the mean daily soil temperature in the field corresponded very closely with the constant soil temperature in the tanks in the greenhouse. These facts seem rather significant to the understanding of the relation of environment to the susceptibility of the hosts to this disease. They indicate, at least, that in this type of disease soil temperature is important as an environmental factor, and, further, that mean soil temperatures over periods of considerable duration are more influential as factors than brief extremes in soil temperature.

SUMMARY

(1) The seedling-blight of wheat caused by *Gibberella saubinetii* is manifest first by blighting before emergence, which results in poor germination, second by blighting after emergence, which is evident by the yellowed and wilted seedlings, and third by stunting the seedling which is due to the weakened root system.

(2) The symptoms of the seedling-blight of corn, caused by this same organism, are, in general, similar to those of wheat.

(3) The invaded tissues in both wheat and corn become reddish brown to carmine red, depending upon environmental factors.

(4) The disease develops from infected seed, scabbed seed in the case of wheat, and infested soils.

(5) The period of seedling infection in both wheat and corn is usually limited to the early seedling stage.

(6) With environmental factors favorable, the extent of blighting and injury from seedling-blight is directly proportional to the amount of infestation.

(7) The parasite in pure culture functions normally over a comparatively wide range of temperature, namely, from 3° to 32° C. The optimum temperature for spore germination, vegetative development, and sporulation is about 24° on unacidified and 28° on acidified media.

(8) Wheat is a low-temperature plant and functions best at a low soil temperature in all stages of its development. On the other hand, corn is a comparatively high-temperature plant and develops best at high soil temperatures.

(9) The temperature of the soil is undoubtedly the most important single factor determining the extent of seedling-blight. The most favorable soil temperature for the blighting of wheat ranges from 12° to 28° C. Below 12° no blight occurred if other factors were favorable. In contrast, the most favorable soil temperature for the blighting of corn ranges from 8° to 20°. Above 24° no blight occurred.

(10) Low soil moistures favor blighting of wheat even at low soil temperatures.

(11) Results from sowings of wheat and corn made at different dates under field conditions agree with those from the greenhouse experiments. Seeding when the soil is cool, that is, spring wheat at the earliest safe date in the spring and winter wheat at the latest safe date in the fall, reduces seedling blight. On the contrary, seeding corn when the soil is warm, that is, at the latest safe date in the spring, reduces seedling-blight.

(12) There are sharp critical temperatures for the production of the blight of both wheat and corn. The mean daily soil temperature in the field corresponds to the constant soil temperature in the soil-temperature tanks. The critical soil temperature for the seedling-blight of wheat is

about 12° C., in both constant soil temperature and mean daily field soil temperature. The critical soil temperature for the seedling-blight of corn is between 20° and 24° under both greenhouse and field conditions.

(13) Infection takes place and the blight progresses, then, at entirely different temperatures with the two different hosts, wheat and corn, inoculated with the same parasite. Hence, the influence of environmental factors on the hosts seems to be the fundamental cause of susceptibility to the disease. The seedlings become susceptible when they are unable to respond favorably to the environment.

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PLATE 1

Seedlings and kernels of Marquis wheat attacked by the wheatscab fungus, *Gibberella saubinetii*.

Seedlings blighted after inoculation in the field with conidia of the parasite grown in pure culture. *a*, Killed before emerging; *b*, killed just after emerging; *c*, killed in first-leaf stage; *d*, badly scabbed kernels, shrivelled and dead; *e*, slightly scabbed, discolored kernels only slightly, if at all, shrunken, but which produce infected seedlings when they germinate; *f*, sound, plump kernels for comparison. ×2.

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PLATE 2

Seedlings of Marquis wheat, (*a*) infected by *Gibberella saubinetii* and (*b*) uninfected, both of the same age.

The infected seedling was from the same inoculation series as those shown in Plate 1, *a*, *b*, and *c*. Note marked reduction in vigor, browning of basal portion, and reduction of root system as well as yellowing of leaves and absence of tillers. The uninfected seedling was from a corresponding uninoculated series. Note general vigor, clean basal portion, abundant vigorous roots, as well as vigorous, healthy leaves and tillers. Natural size.

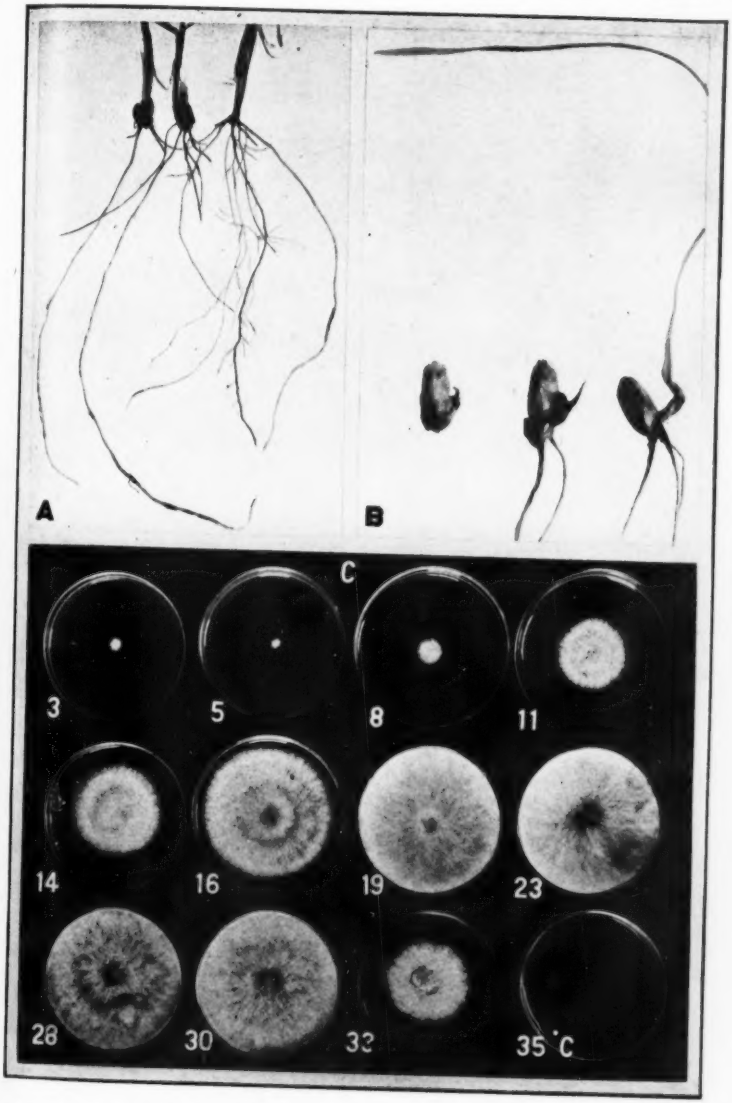
PLATE 3

Wheat seedlings attacked by wheatscab fungus, *Gibberella saubinetii*, and Petri-dish cultures of the same fungus incubated six days at different temperatures.

A. Winter wheat (Turkey) seedlings from artificially inoculated seed, taken from the field late in the fall. The blackened, rotted roots resulted from the progress of the disease early in the season while the soil was warm. The new, white, healthy roots developed later in the season while the soil was cool.

B.—Blighted seedlings of Marquis wheat from artificial inoculation, taken from the field in the spring. The first two seedlings (left) represent typical blighting before emergence. The seedling on the right was blighted in the first-leaf stage.

C.—Relation of temperature to the vegetative development of *G. saubinetii*. Petri-dish cultures of the fungus incubated six days on unacidified, potato-dextrose agar at temperatures from 4° to 35° C., as indicated by figure below each culture.


A
B
C
3
5
8
11
14
16
19
23
28
30
32
35°C

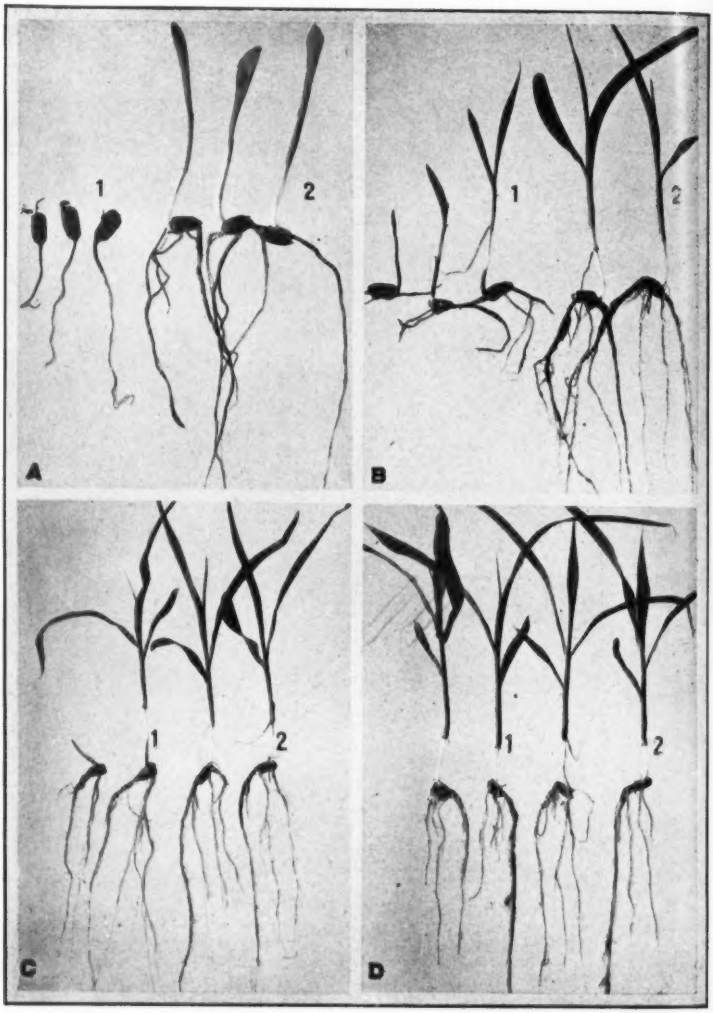

1
2
A
1
2
B
1
2
C
1
2
D

PLATE 4

Representative corn seedlings, from inoculated and uninoculated seed, grown at different soil temperatures.[1]

A.—Plants grown at a soil temperature of 12° C. Plants from the inoculated seed were all killed before emerging.

B.—Plants grown at a soil temperature of 16° C. Plants from the inoculated seed were badly diseased. About half of them blighted soon after emerging.

C.—Plants grown at a soil temperature of 20° C. Plants from the inoculated seed almost as badly diseased as those grown at 16° C., represented in B.

D.—Plants grown at a soil temperature of 24° C. Plants from the inoculated seed were healthy except for a few minor root lesions.

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[1] In each set of plants from A to D, (1) represents typical plants from seed inoculated with conidia of *Gibberella saubinetii* and (2) represents seedlings of the same age and from the same seed uninoculated.

PLATE 5

Influence of soil temperature and moisture on the development of seedling-blight of Marquis wheat.[1]

A.—Seed sown in soil wet to 30 per cent of its moisture-holding capacity. Note percentage of blight which developed at 8° C.

B.—Seed sown in soil wet to 45 per cent of its moisture-holding capacity. Note decrease of blight which developed at 8° C.

C.—Seed sown in soil wet to 60 per cent of its moisture-holding capacity. No blight developed at 8° C., and less at all temperatures than in the drier soils.

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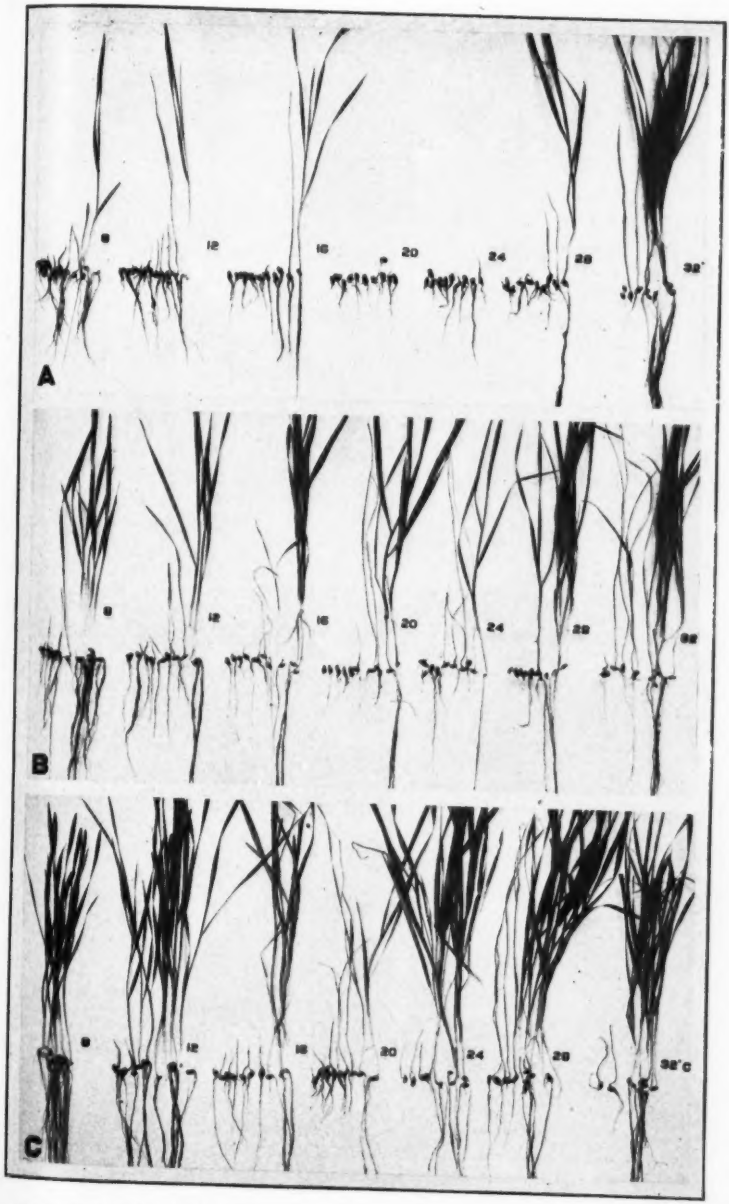
[1] The 10 seedlings in each group represent the proportion of healthy and blighted seedlings from a series of 200 plants grown at each soil temperature from seed inoculated with *Gibberella saubinetii*.


A
B
C
8
12
16
20
24
28
32°C

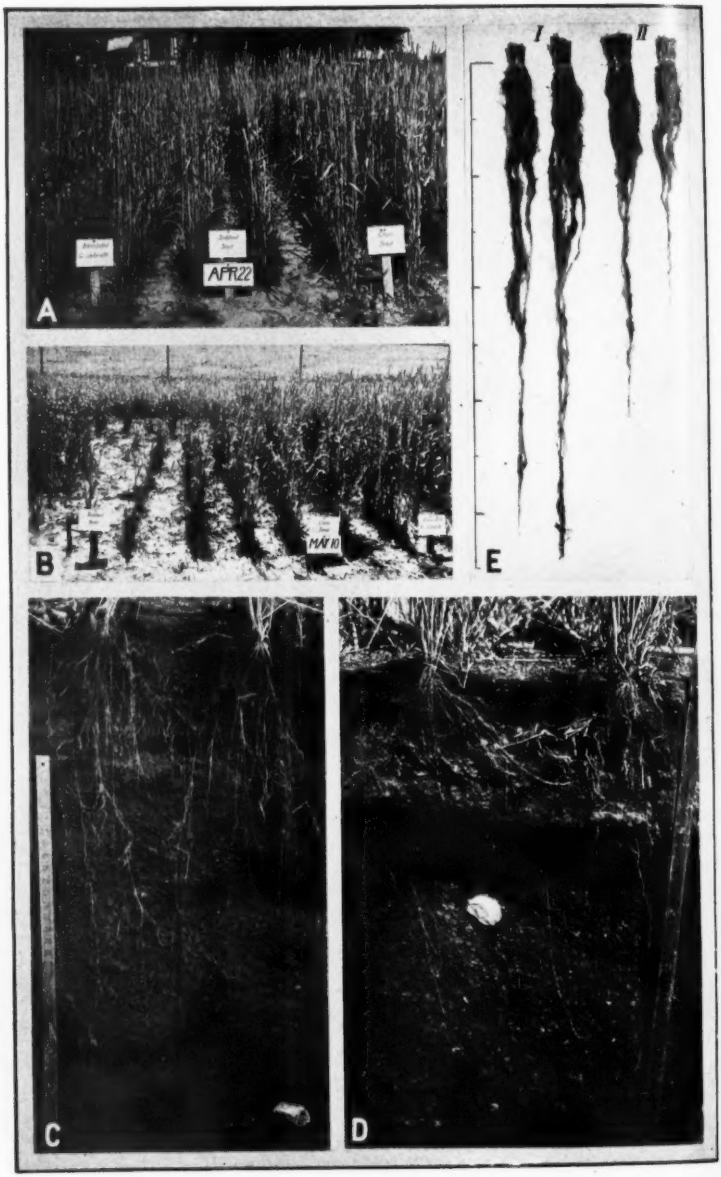

A
APR 22
B
MAY 10
E
I
II
C
D

PLATE 6

Relation of date of seeding to the development of seedling-blight of Marquis wheat.

A.—Wheat plants from inoculated, scabbed, and clean seed sown April 22, when the soil temperature was below 12° C. Note the uniformly good stand from all three lots of seed.

B.—Wheat plants from inoculated, scabbed, and clean seed sown May 10, when the soil temperature was above 12° C. Note the greatly reduced stand from the inoculated seed and especially from the scabbed seed.

C.—Root development of wheat sown April 22. Left, uninoculated; right, inoculated with *Gibberella saubinetii*. Note the large root systems in each.

D.—Root development of wheat sown May 10. Left, uninoculated; right, inoculated with *G. saubinetii*. Note that the root development is much less extensive than on the plants from the April 22 seeding shown in C. See E for the detailed comparison of the root systems.

E.—Root systems of the four lots of spring-wheat plants shown in position in C and D. Each bundle contains the roots of five plants. (1) Sown April 22; left, uninoculated; right, inoculated. (2) Sown May 10; left, uninoculated; right, inoculated. Note the reduction in root systems in (2) right, inoculated seed sown May 10, when the mean soil temperature was above 12° C. In contrast, note the lack of reduction in (1) right, where the seed was inoculated and sown April 22, when the soil temperature was below 12° C.

FURTHER STUDIES IN PHOTOPERIODISM, THE RESPONSE OF THE PLANT TO RELATIVE LENGTH OF DAY AND NIGHT [1]

By W. W. GARNER, *Physiologist in Charge*, and H. A. ALLARD, *Physiologist, Tobacco and Plant Nutrition Investigations, Bureau of Plant Industry, United States Department of Agriculture*

INTRODUCTION

In an earlier paper (*7*)[2] considerable data were presented tending to show that the length of day exercises a remarkable regulatory action in initiating or inhibiting sexual reproduction in plants. In a number of species studied it was found that ordinarily the plant can attain the flowering and fruiting stages only when the length of day falls within certain limits, so that in such cases flowering and fruiting occur only at certain seasons of the year. In this respect some species and varieties respond to relatively long days while others respond to short days. Moreover, some plants are much more sensitive to change in length of day than are others. In the absence of the particular day length favorable to sexual reproduction vegetative development may continue for a more or less indefinite period, thus frequently leading to the phenomenon of gigantism. It was discovered, also, that exposure to a daily light period intermediate between that favorable only to vegetative development, on the one hand, and that favoring only flowering and fruiting on the other hand, tends to cause both forms of activity to progress simultaneously. This combined form of activity constitutes what is commonly known as the "everflowering" or "everbearing" behavior. It was suggested that probably the seasonal range in length of day is an important factor in the natural distribution of plants and that in agricultural practise the correct time for planting many crop plants may be largely conditioned by the prevailing length of day. To designate the response of the plant to length of day the term "photoperiodism" was suggested.[3] The data on which these conclusions are based were obtained chiefly by use of dark chambers into which the test plants could be placed for a portion of the day, thus reducing the number of hours of illumination received during the relatively long days of summer. Brief mention also, was made of greenhouse experiments conducted during the winter months, in which electric light was used to prolong the daily period of illumination. The results of these latter tests confirmed those previously obtained by use of the dark chambers. Oakley and Westover (*18*) have recently reported an interesting application of these principles as a means for the quick identification of seed of different alfalfas.

[1] Accepted for publication May 10, 1922.
[2] Reference is made by number (italic) to "Literature cited," p. 919–920.

[3] The authors are indebted to Mr. O. F. Cook, of the Bureau of Plant Industry, for suggesting the term photoperiodism, which seems to meet satisfactorily all requirements as to both aptness and simplicity.

In connection with the discussion of the literature bearing upon the subject which was presented, attention is here called to an article by Klebs (*10*) on flower formation in Sempervivum, published in 1918, which had not become accessible to the writers at the time the previous paper was written. Following methods somewhat similar to those previously employed by Bonnier, Bailey, Rane, and Corbett, as briefly outlined in our former paper, Klebs showed that Sempervivum, which normally flowers in June, could be forced into flowering in winter, either by means of continuous electric illumination for a few days or by increasing the daily illumination period to more than 12 hours. The Osram lamp was used both for continuous illumination and for daily illumination periods of different duration. This result with Sempervivum is essentially the same as that obtained by Bailey and by Rane with spinach (*Spinacea oleracea* L.), but Klebs, perhaps, made a more complete analysis of the response and his data are more nearly quantitative in character. He also studied the effects of change in intensity and quality of the light on flowering in Sempervivum. Light seems to be essential for the formation of flower primordia. The response of Sempervivum to differences in light exposure is interpreted by Klebs as supporting the theory previously advanced that flowering is the result of increased concentration of the cell sap, particularly with respect to carbohydrates. In summarizing, it is stated that in flowering the quantity of the light energy is of decisive importance.

It is especially desirable, also, to call attention here to the remarkable life histories of two small marine worms, *Convoluta roscoffensis* and *C. paradoxa*, as worked out by Keeble (*9*, *p. 31*) and others. A curious form of symbiosis with a green and a brown alga, respectively, is involved, so that these creatures have received the designation "plant animals." The movements of these worms, which live on the seashore, correspond with the incoming and outgoing tides. Thus, *C. roscoffensis* regularly sinks below the surface of the sand with the incoming tide and emerges as the tide recedes. This synchronism with tidal movement has been shown to be due to the alternate exposure to light and darkness as the tide recedes and again advances. What is of special interest here, however, is the remarkable fact that with this organism reproductive activities occur chiefly at 2-week intervals, beginning with the onset of spring tides. This is due to the fact that at this season of the year low water occurs only once during the day, the other period coming at night, with the result that the worms receive daily only about six hours of sunlight. Egg-laying reaches its maximum when the animals are subjected daily to one short spell of six hours' light-exposure followed by a long spell of eighteen hours' dark exposure. But—and the fact is remarkable—these conditions of light and darkness are precisely those to which *C. roscoffensis* is exposed during the spring tidal periods at which its eggs are laid habitually.

The observations and conclusions recorded in the former paper concerning the regulatory action of the relative length of day and night on flowering and fruiting as against the purely vegetative form of activity have been confirmed and considerably extended by further study of the subject, as will be outlined in this paper. In view of the marked influence of day length on sexual reproduction it seemed likely that plants would be found to respond to this influence in other ways, and, accordingly, a series of experiments was made to test this possibility. It was found, in fact, that the plant is capable of responding in many ways to change in the duration of the daylight period. Thus, most if not all outstanding

phenomena of periodicity seem to be more or less influenced by the seasonal change in length of day. Moreover, some features of plan development not so definitely periodic in character appear to be related to the duration of the daylight period. Because of the wide field covered a great deal of experimental data must be accumulated before a full discussion of these various responses can be undertaken, and it is not practicable at this stage to attempt to correlate the extensive literature on the different features of plant development with the preliminary observations which have been made. In the present paper a somewhat more detailed discussion of the formation of tubers, bulbs, and thickened roots in relation to sexual reproduction will be undertaken. Only briefer mention of other features of the photoperiodic response will be made, reserving fuller consideration for the future. Perhaps the principal value of the limited number of observations which have been made on various forms of response, viewed as a whole, is that they may be made the basis of a working hypothesis as to the nature of some of the internal processes involved in photoperiodism, thus suggesting more systematic biological and biochemical studies along definite lines. The wide extent and great variety in form of the photoperiodic response verifies in most striking manner the soundness of the modern view, the most consistent supporter of which perhaps has been Klebs, to the effect that environment through its action on internal conditions governs the form of expression in the plant, subject only to the specific limitations imposed by heredity.

FURTHER OBSERVATIONS ON FLOWERING AND FRUITING

Woody perennials, particularly the larger-growing forms, do not lend themselves so readily to the methods of study which have been followed, so that the data thus far accumulated have reference mostly to annuals and herbaceous perennials, though a number of shrubs and dwarf trees are now under observation. In the following experiments the methods followed were essentially the same as those described in the former paper; namely, the use of light-proof houses into which the plants could be placed for a portion of the day during the open growing season and the use of electric light in the greenhouse for a portion of the night during the winter months. The average intensity of the electric illumination maintained in the vicinity of the plants in the greenhouse was approximately 3 to 5 foot-candles and the lights (40-watt mazda bulbs) were on from sunset till midnight each day. In reducing the daylight period the plants in most experiments received sunlight only from 10 a. m. to 3 p. m. for the 5-hour exposures; from 5.30 a. m. to 3.30 p. m. for the 10-hour exposures; from 5.30 a. m. to 5.30 p. m. for the 12-hour exposures; from 5.30 a. m. to 6.30 p. m. for the 13-hour exposures.

Seed of *Amaranthus hybridus* L. which was sown in metal buckets July 8 had germinated by July 11. Under daily light exposures of 10, 12 and 13 hours the first blossoms opened August 6 while the average heights of the plants, 20 to 30 in number, were 13 to 14 inches, 16 to 17 inches, and 15 to 16 inches, respectively. With 5 hours of light daily, first blossoms were open August 14 and the average height was 8 to 9 inches. The controls exposed to the full natural day length first showed blossoms August 23 and the average height was 26 to 27 inches.

Kulthi bean (*Dolichos biflorus* L.), planted May 29, showed open blossoms July 21 under a 13-hour daylight exposure. Flowering was sparse and temporary, followed by rapid growth. On September 1 flower buds were again evident. The controls first showed open blossoms August 2 and also were again showing flower buds on September 1. It appears that a day length somewhat less than 13 hours is required for quick and profuse flowering in this species.

Peruvian flour corn (*Zea mays* L.), supplied by the Office of Cereal Investigations, Bureau of Plant Industry, was planted May 29 in boxes 10 inches square and 3 feet long. Under a daylight period of 13 hours the plants were shedding pollen July 26 and under natural daylight conditions on August 24. The respective heights of the plants were 71 and 92 inches.

A very late-maturing variety of corn from Mexico, known as Tuxpan, planted May 22 in boxes as above, was shedding pollen August 6 as a result of receiving a 10-hour light exposure and the average height was 50 inches. Under a 13-hour light exposure pollen was falling August 14 and the average height was 53 to 54 inches. The controls were shedding pollen September 13 and the height was 86 inches. It is worthy of note that at the middle of September the 10-hour day plants, as well as the controls, were decidedly greener in color than those exposed to a 13-hour day.

Tests were made with several sorghums (*Holcus halapensis* L.) from tropical Africa and India, seed of which was furnished by the Office of Forage Crop Investigations, of the Bureau of Plant Industry. Seed was sown June 17. The pots containing the plants were transferred to the greenhouse October 11 to prevent injury from cold weather. The results of the tests are summarized in Table I.

In the former paper (7) the behavior of buckwheat (*Fagopyrum vulgare* Hill) in the greenhouse in winter was briefly described. Under the natural day length the plants completed the life cycle within a few weeks, attaining a relatively uniform height of only 24 inches. Increase in the duration of the daily light period to about 18 hours with electric light gave marked irregularity in height attained and degree of flowering. Some individuals attained a height of 9 feet or more, and all acted as typical ever-bloomers, with indeterminate growth characteristics. Repetition of the experiment in summer (seed planted May 18) gave similar results except that the height attained by the plants under the longer natural day length was increased to between 4 and 4½ feet. Outdoor tests also were made in the summer under regulated day lengths of 5, 10, and 13 hours, with controls, all plantings being made June 8. Flowering began in the controls on July 6; in all other cases on June 30. Under a daylight period of 5 hours the plants were very small and soon died, after having produced a few seeds. With 10 hours of light daily the plants lived longer and attained a height of 24 inches. Under the 13-hour exposure the plants were slightly taller and more seeds were produced. The controls averaged 36 inches in height and fruited freely. Thus, it is easily seen why buckwheat makes best growth in high latitudes.

TABLE I.—*Effect of length of day on growth of sorghums from tropical Africa and British India*

S. P. I. varietal number.[1]	Point of origin.	Number of plants grown.			Date of shedding first pollen.			Average height August 17 (inches).			Stooling or branching, August 17.		
		10-hour day.	13-hour day.	Control.	10-hour day.	13-hour day.	Control.	10-hour day.	13-hour day.	Control.	10-hour day.	13-hour day.	Control.
37114	Kano, North Nigeria, lat. 12° N.	5	3	4	Aug. 2	Nov. 29	Dec. 14	52	30	27	Marked.	Slight.	None
39449	Calulo, Angola, lat. 15° S.	12	6	5	3	.....	14	43	33	23	None...	None..	Do.
39451	Calulo, Angola.	5	5	5	4	Dec. 17	17	52	33	26	...do....	...do...	Do.
43606	Caunpore, India, lat. 20° N.	5	3	3	9	.....	Sept. 25	65	66	40	...do....	...do...	Do.
39450	Togo, German West Africa, lat. N. 8°.	5	9	7	2	Oct. 23	Nov. 15	70	42	34	Marked.	...do...	Do.
39450	Calulo, Angola.	4	5	5	3	Dec. 15	Dec. 17	54	32	27	None ..	...do...	Do.

[1] The varietal numbers are those of the Office of Foreign Seed and Plant Introduction, Bureau of Plant Industry.

Roots of perennial wild sunflower (*Helianthus giganteus* L.) transferred to the greenhouse in October soon developed vigorous shoots. Under natural daylight conditions flower buds appeared early in April and open blossoms in May. With the natural daylight period lengthened by use of the electric light till May 26, flowering was inhibited and there were no indications of blossoming as late as July 1.

Another wild sunflower, *Helianthus angustifolius* L., an eastern and southern species, was planted in the electrically lighted house January 27. Under the long daily light exposure the plants grew to a height of 6 to 7 feet without flowering at any time during the year. Specimens transferred to a daily light exposure of 10 hours, beginning September 2, began flowering October 4 (Pl. 2, A). Another lot of the plants exposed to the natural day length, beginning September 2, also flowered as a result of decreasing day length but much later than those under the 10-hour exposure. The plants remaining in the electrically illuminated house finally formed flower buds in November, but under the combined influence of the weak electric light at night and the natural light of the short winter days these buds were prevented from unfolding and remained in a practically dormant condition throughout the winter.

Cosmos bipinnata Cav., planted November 1, was in flower December 22 and attained a final height of 30 inches under the normal day length. Continuing the light period till midnight by means of the electric light until arrival of the long summer days inhibited flowering. Growth continued until early October, and the plants had attained a height of 15 feet when forced into flowering by the decreasing day length.

Klondike cosmos (*Cosmos sulphurea* L.) was planted April 22 and had germinated April 25. Under a 10-hour day beginning July 6 flower buds were showing July 19, and the first blossoms were open August 1. The control plants exposed to the natural length of day first showed flower buds October 1, and the first open blossoms appeared October 14.

Corms of blazing star (*Liatris graminifolia* Walt.) were transplanted to metal buckets March 27. Under a 10-hour day the first blossoms opened

June 21, the plants averaging 17 inches in height. Under a 13-hour day blossoming began July 22, and the average height was 24 inches. The controls began flowering August 26 and were slightly taller than the 13-hour day plants. In the following season a second lot of corms were transplanted from the field May 19 and exposed to different day lengths. Under a 10-hour day flower buds were showing June 6, and the first open blossoms appeared July 2. The average height of the plants was 12 inches. Under a 12-hour day flower buds could be seen June 6, and the first blossoms unfolded June 30, when the plants had attained a height of 12 inches. The controls were showing flower buds July 22 and first open blossoms September 12. The average height was 35 inches.

Tithonia rotundifolia (Mill) Blake, planted January 4, was in bloom March 14 under natural daylight, having attained a height of 48 inches. In the greenhouse electrically lighted at night the height on March 14 was 27 inches and there were no indications of flowering. Blossoming was inhibited indefinitely under these conditions. Seed were again sown April 6. The plants exposed to a 10-hour day beginning June 3 were showing flower buds July 27 and open blossoms on August 13. The control plants under the full day length showed no flower buds as late as September 22.

Roots of sorrel (*Rumex acetosella* L.) were transferred to the greenhouse October 12. Under natural day length aerial development was limited to abundant leaf formation, while under the artificially lengthened illumination period flowering stems were formed and pollen was falling January 19. Thereafter these latter plants continued as typical everbloomers. The plants under the short-day exposure, on the other hand, were very active in the development of underground stems, the soil of the container becoming thickly studded with this type of growth. When grown in the open bed in the greenhouse under the short-day conditions the plants produced underground stems 2 feet or more in length.

Plants of roselle (*Hibiscus sabdariffa* L.) were subjected to a 10-hour day when about 10 inches high, beginning July 20. First blossoms appeared September 11, whereas the control plants did not flower till early November.

Cuttings of smartweed (*Polyganum* sp.) were set in moist sand June 30. Under a 10-hour light exposure the plants were in blossom July 21, while the controls showed no indications of flowering on August 18. The respective heights of the plants July 28 were 14 and 9 inches.

A late fall variety of chrysanthemum was exposed to a 10-hour day, beginning May 12, and was in blossom July 28, while the control plants, of course, did not flower till late fall. Under a 13-hour exposure flowering was about 3 weeks later than under the 10-hour exposure. The 10-hour day plants flowered freely and the blossoms were normal.

A very late variety of dahlia, known as John Ehlich, was placed under a 10-hour day, beginning May 12, and the first blossom opened July 8. Under the natural day length the first blossom opened September 27.

Specimens of poinsettia (*Euphorbia heterophylla* L.), 8 to 10 inches high, exposed to 10 hours of light daily after July 9 soon flowered, and in 5 to 6 weeks the tops of the plants were gorgeously colored. (Pl. 19, A.) Similar plants exposed to 12 hours of light daily blossomed September 3, but the upper leaves reddened very slowly. The controls did not flower till November. The 12-hour plants eventually produced numerous viable

seed, whereas the 10-hour plants produced no seed. One of the control plants was transferred October 2 to the greenhouse electrically illuminated at night and under these conditions continued in the vegetative state without flowering throughout the winter.

Roots of goldenrod (*Solidago juncea* Ait.) were transferred to the greenhouse November 15, one lot receiving only natural daylight while the other lot received the electric illumination from sunset till midnight. Under the lengthened illumination period flowering began March 15. Beginning March 10, the plants in the control house were placed in a dark cabinet for a portion of each day so that they received only 7½ hours of light daily. In one instance a short, weak flowering stem developed as a result of the stimulus from the natural increase in day length before the transfer to the dark cabinet was begun. The remaining plants formed no stems but continued to form rosettes of leaves as the older leaves perished (Pl. 5, B). This type of activity, with complete suppression of stem development, persisted throughout the duration of the experiment, a period of more than 18 months.

Cuttings of hedge bindweed (*Convolvulus sepium* L.) exposed to 10 hours of light daily, beginning May 13, developed no flower buds, whereas the controls, exposed to the full day length, were in blossom June 30. Other lots of cuttings were exposed to different daylight periods, beginning June 7. The controls, as well as the plants receiving 13 hours of light daily, formed numerous flower buds and began blossoming June 28 to 30. Under a 12-hour day only three flower buds were formed on two plants, and under an 11-hour day no flower buds at all appeared.

Seed of winter and spring varieties of wheat (*Triticum vulgare* L.), rye, (*Secale cereale* L.), oats (*Avena sativa* L.), and barley (*Hordeum vulgare* L.) furnished by the Office of Cereal Investigations, Bureau of Plant Industry, were planted in the electrically lighted and the control greenhouse units on November 29. The greenhouse was kept relatively warm, the temperature usually running 55° to 60° F. at night and 70° to 80° during the day. The behavior of the plants under the two conditions of illumination is summarized in part in Table II.

These results with the small grains are too limited in scope and extent to justify final conclusions, but they seem to show clearly that detailed study of these crops in their reactions to day length would give very interesting and valuable results. It appears that a fundamental distinction between the winter and spring types as such rests on the rapidity with which the latter respond to the increasing day length of spring.[4] The forcing action of the electric light on the spring types resulted in sparse fruiting, possibly because of the low intensity of the light.

[4] Since this paper was written Wanser has published in Science (WANSER, H. M. PHOTOPERIODISM OF WHEAT; A DETERMINING FACTOR IN ACCLIMATIZATION. *In* Science, n. s., v. 56, p. 313–315. 1922) an interesting account of a preliminary experiment dealing with photoperiodism in wheat, in which distinctive photoperiods are found for the jointing and the heading stages in winter wheat. The fundamental differences between winter and spring varieties of the small grains in their response to length of day brought out in the above data are confirmed by Wanser's results with wheat.

TABLE II.—*Effect of length of day on growth of winter and spring varieties of wheat, rye, oats, and barley.*

Crop.	Date of first heading.		Average height at time of heading.		Average height, May 11.		Average number of basal branches.	
	Under electric light.	Control.	Under electric light.	Control.	Under electric light.	Control.	Under electric light.	Control.
			Inches.	*Inches.*	*Inches.*	*Inches.*		
Wheat, Marquis (spring), C. I. 3641 [1].	Jan. 24	Apr. 8	28	51	36	56	8	25
Wheat, Purple Straw (winter)	Mar. 17	Mar. 23	46	41	51	52	31	13
Rye (spring), C. I. 169.	Jan. 6	Mar. 29	16	25	24	56	6	30
Rye, Abruzzi (winter), C. I. 40	Jan. 24	Mar. 23	27	24	62	61	25	11
Oats, Swedish Select, (spring), C. I. 1426	Jan. 10	Mar. 28	15	51	36	72	28	19
Oats, Winter Turf, C. I. 274–20	Feb. 25	Apr. 8	49	44	61	51	33	33
Barley, Manchurian (spring), C. I. 19A625	Feb. 1	Mar. 15	36	46	40	46	16	26
Barley, (Tennessee Winter), C. I. 257	Apr. 26	Apr. 25	.....	.....	36	36	.....	.....

[1] The varietal numbers are those of the Office of Cereal Investigations, Bureau of Plant Industry.

Young plants of arrowhead (*Sagittaria latifolia* Wild), taken from a marsh, were transplanted to 3-gallon metal buckets with perforated bottom and containing garden soil maintained at approximately optimum moisture content for such plants as soybeans. Similar lots of plants also were transplanted to 3-gallon earthen jars containing 6 inches of soil covered to a depth of 4 to 5 inches with water. Under a 10-hour day, beginning May 3, two plants in a metal bucket flowered June 14 and 17, respectively, and three individuals in an earthen jar flowered June 28, July 5, and July 9, respectively. Two controls in each of two earthen jars, exposed to the full day length, flowered August 19, 22, 24, and 27, respectively. The plants in the metal bucket were restored to the full daylight period June 17, and one of these flowered the second time on August 22. In a second series, transplanted May 15, three plants in each of two earthen jars exposed to 10 hours of light daily, beginning May 15, began flowering June 11 and 14, respectively. Under 10-hour day, beginning June 13, four plants in an earthen jar flowered June 27, 28, 29, and 30, respectively, while under a 12-hour day one of three plants flowered on June 30 and the other two on July 2. Under a 10-hour day, beginning June 23, two plants in a metal bucket flowered July 5. The controls of the second series, transplanted May 15 to an earthen jar and to a metal bucket, had not flowered September 20.

Very young plants of jewelweed (*Impatiens biflora* Walt) were transferred from the swamp to 3-gallon metal buckets April 12, five plants being set in each bucket. Under a 10-hour day flowering began June 7. The controls began flowering July 6.

Morning-glory (*Ipomoea hederacea* Jacq.) was planted June 8 and had germinated June 11. Under a 10-hour day flower buds appeared July 2 and the first open blossoms were in evidence July 10 (Pl. 2, B).

The controls showed flower buds August 25 and open blossoms September 9. The 10-hour light exposure produced a decidedly darker shade of green in the foliage leaves than did the full summer day length. These short-day plants continued to grow slowly through the flowering period and were still green September 23.

Seeds of Brazilian morning-glory (*Ipomoea setosa* L.) were planted June 8, and the seedlings had emerged from the ground on June 11. Exposed to 10 hours of light daily, the plants were showing flower buds July 5 and the first blossoms opened July 19. On the controls flower buds could be seen August 25 and the first blossoms opened September 9.

The dwarf morning-glory, *Convolvulus tricolor* L., was planted June 8 and had germinated June 11. Under a 10-hour day the plants were unable to flower but remained green and continued to grow vigorously. The controls under the natural length of day were showing flower buds August 1 and first open blossoms August 11. After a period of flowering through August these plants reverted to the purely vegetative phase of activity after the first week in September, assuming a condition comparable with that of the plants exposed to a 10-hour day.

Moonvine (*Calonyction aculeatum* (L.) House) planted June 8 had germinated June 11. With 10 hours of light daily flower buds appeared July 15 and open blossoms August 5. On the controls flower buds could be seen July 23 and open blossoms August 16.

Seeds of cypress vine (*Quamoclit pennata* (Desr.) Voigt) were planted June 8 and appeared above ground June 11. Under 10 hours of light daily, flower buds were showing June 22 and the first blossoms were open July 5. On the controls the first open blossoms appeared August 3. The short-day plants grew more rapidly and were darker in color than the controls exposed to the full day lenght.

LONG-DAY AND SHORT-DAY PLANTS AND THE CRITICAL LENGTH OF DAY FOR FLOWERING

As pointed out in the earlier paper and further illustrated in the preceding data, the plants studied tend to arrange themselves into two groups. One of these groups consists of species that are caused to flower by the action of short days while the other includes those species that are forced into flowering through the action of long days. For convenience the first named group are spoken of as short-day plants while the second group are designated as long-day plants. At first sight it would seem that these two groups of plants are diametrically opposed in their response to length of day, but detailed study of the two groups indicates that the difference is one of degree rather than of kind. In fact, classification into the two groups is more or less arbitrary. In the case of such plants as Cosmos and Bidens, flowering is inhibited by a daily light exposure much in excess of 12 hours' duration, while vegetative development promptly gives way to flowering when the light period is reduced to 12 hours or less. These plants will flower even when receiving only a few hours of light daily; in other words, it is not possible to reduce the light duration sufficiently to prevent flowering without killing the plants. On the other hand, Solidago and Hibiscus are readily prevented from flowering by reducing the light period to something less than 12 hours, although under these conditions they may continue to live and may even continue development in certain directions. These plants are not inhibited from flowering by increasing the light duration beyond the normal.

The important point is that the inhibition of flowering in the first case by a long light period is not of the same sort as the inhibiting effect of a short light period in the second case; that is, the inhibition in the two cases results in different alternative forms of vegetative activity, as will be shown in later paragraphs. There are, moreover, plants which may be said to occupy an intermediate position in that it is possible to have a day length too long as well as one too short to induce flowering. *Mikania scandens* L., briefly discussed in our former paper (7), is an example of this type. In the wild state Mikania regularly flowers in late July and through August, and if kept in the greenhouse through the winter it also usually flowers very sparsely in the spring. Seedlings from a planting made December 10 were unable to flower under the influence of the lengthened daily light period in the electrically illuminated greenhouse, while similar plants in the control greenhouse flowered at the usual time in August of the following summer. On the other hand, this species was unable to flower through the summer or fall under day lengths of 5, 10, and 13 hours' duration. The Biloxi variety of soybeans (*Soja max* (L.) Piper), discussed in detail in the former paper (7), occupies a position slightly below the intermediate position of Mikania in response to day length. In this case flowering is readily inhibited by a day length in excess of 13 hours. On the other hand, with very short day lengths only a very few cleistogamous flowers and fewer seed are developed but the reproductive phases apparently can not be entirely suppressed.

Thus, there are species occupying various positions within the annual range of day length with respect to the initiation of reproductive activities, and there is no definite line of division between long-day plants and short-day plants. An illumination period on one side of the critical duration for flowering promotes certain forms of vegetative activity, while a light period lying on the other side of the critical promotes other forms of vegetative activity, as will be shown under the discussion of apogeotropism (p. 886).

Not only do plants differ markedly as to the particular length of day most favorable for flowering but they also differ widely as to the narrowness of the range in day length which will permit of flowering. Experiments with Mikania, referred to above, indicate that under ordinary conditions this plant will readily flower only under a day length ranging but little beyond an hour on either side of 14½ hours, which is approximately the optimum for flowering. Buckwheat flowers readily under a daily illumination period ranging at least from 5 hours up to 18 or 20 hours and probably even under continuous illumination, notwithstanding the fact that the extent of vegetative development and life duration are profoundly affected by this range in the length of the light period. While there is a certain degree of antagonism or incompatibility between the vegetative and reproductive phases of activity, the two obviously are not necessarily affected to the same degree by a given change in duration of the light period. *Viola papilionacea* Pursh will flower under all lengths of day met with in temperate regions except for a short period in midwinter. In the broadest sense the plant will flower continuously for about 10 months of the year, a conspicuous example of everblooming. During the summer months, however, only the cleistogamous type of flower is seen while in spring and fall only the showy blue, chasmogamous blossoms develop. By maintaining a light period equivalent to the long summer days the cleistogamous flowering continues indefinitely and, similarly, a considerably shorter light period will maintain the

open type of flowering indefinitely, thus illustrating a narrower type of everblooming (*8*). In this case the whole effect of the range in length of day from February to the summer solstice is merely to change the type of blossom (involving change in relative fertility).

Thus, beginning with the equatorial length of day of 12 hours as the standard, it may be said that a group of plants normally will flower under any range downward to less than 6 hours, while another group will flower under any range upward to at least 18 hours and probably up to continuous illumination. Other plants will flower only within a comparatively narrow range on either side of the 12-hour standard. Still others are capable of flowering throughout these ranges, their response being quantitative rather than qualitative in character.

BALANCE BETWEEN FLOWERING AND VEGETATIVE ACTIVITY

Within the range of duration of light exposures which will admit of alternative forms of expression there are in most cases certain exposures favorable only to sexual reproduction and other exposures favorable only to vegetative activity. That is, there are more or less definite optima in light exposures for the two alternative forms of expression. The question arises as to the response of the plant to light exposures intermediate between those specifically favorable to the two types of activity. In reality the effects of these intermediate exposures are important and are both quantitative and qualitative in character. There are two aspects of the problem. Under artificial control, fixed day lengths of intermediate duration may be studied, whereas, in nature, there is a graduated change from one optimum toward the other and of course the change may be in either direction.

One of the effects of an intermediate light exposure is a tendency toward the condition of everflowering in which the plant divides its activity between the vegetative and the reproductive phases of development. As the day length approaches the optimum for flowering, the vegetative phase of activity is reduced more or less and vice versa. Thus, the Yellow Dent variety of corn grown in summer in the greenhouse, with electric light at night to give an illumination period of 18 hours, produced larger, taller, and longer-lived stalks while the ears were longer, with longer stems, but were poorly filled as compared with the controls exposed to the normal summer day length. Again, under a 10-hour day Biloxi soybeans gave per plant a dry weight of 10.9 gm. of stalk and 36.6 gm. of seeds, a ratio of 1 to 3.3. The corresponding values under a 13-hour day were 65.8 gm. of stalk and 95.3 gm. of seeds, a ratio of 1 to 1.4. Under the 10-hour day growth ceased as soon as flowering began, but under the 13-hour day there was a tendency toward everbearing, for growth and fruiting proceeded simultaneously. A considerable volume of data which need not be considered in detail here has been obtained with soybeans grown under artificially regulated day lengths and planted in the field at stated intervals during the season, all of which further exemplify this principle of the influence of intermediate day lengths on the quantitative relation between vegetative and reproductive activities.

TABLE III.—*Effect of length of the daily light period on the size of seed in different varieties of soybeans*

Length of daily light exposure.	Average weight of 500 seeds.			
	Mandarin.	Peking.	Tokyo.	Biloxi.
Germinated May 17:	*Gm.*	*Gm.*	*Gm.*	*Gm.*
Full daylight throughout, 15 to 11½ hours	100.0	43.2	110.4	Did not mature.
7 hours throughout	67.6	48.4	130.6	131.2
5 hours till 1 week after flowering; full daylight thereafter	85.8	36.0	60.4	88.4
Full daylight till flowering; 7 hours thereafter	.....	49.2	.....	.....
Full daylight till flowering; 5 hours thereafter	.....	37.0	105.0	.....
Germinated June 15:				
Full daylight throughout, 15 to 11½ hours	93.8	37.4	99.8	Did not mature.
12 hours throughout	89.4	62.8	125.8	129.8
Darkness 10 a. m. to 2 p. m. (and at night) throughout	.....	30.0	.....	.....

It has been found, also, that the size of the individual seed is influenced by the relation of the prevailing light period to the respective optimal period for vegetative and reproductive development. The data presented in Table III throw light on this question. It is seen that in the early variety of soybeans, Mandarin, which fruits readily in the longest days of summer, shortening the light period to 12 hours or less reduced the size of the seed and restoring the plant to the full summer daylight period after flowering had occurred tended to offset the unfavorable influence of the previous exposure to 5 hours of light daily. With the later varieties, requiring shorter days for flowering, the results are quite different. For these a 12-hour exposure gives decidedly larger seeds than the full day length of summer and for the Tokyo and Biloxi a 7-hour day gives fully as large seed as a 12-hour day. A 5-hour light period till flowering, followed by exposure to the full day length, reduced the size of the seed markedly in all except the early variety. A midday period of darkness acted unfavorably. All these data harmonize with previous results on the action of regulated day lengths in initiating or inhibiting flowering and fruiting in these varieties of soybeans.

An intermediate light exposure tends to delay the time of flowering, and as the light period is advanced toward the optimum for vegetative development flowering is more and more delayed, the tendency being toward more or less indefinite inhibition. Biloxi soybeans which germinated June 1 began flowering June 27 under a 10-hour day, while the first blossoms appeared July 13, 16 days later, under a 13-hour day. Other plantings gave very similar results. It has previously been shown that a day length of 14 hours or more delays flowering indefinitely in the Biloxi. The Peking variety planted on June 18 began flowering July 14 under a 13-hour day as well as under a 10-hour day for the reason that the 13-hour day length does not materially exceed the optimum for flowering in this variety. It should be noted, however, that development and ripening of the seed of the Peking are decidedly hastened by

the 10-hour day as compared with the 13-hour day. By referring to Table I it will be seen that a 13-hour day delayed flowering in varying degrees in different varieties of sorghum as compared with a 10-hour day. As previously noted, flowering in chrysanthemum and poinsettia, also, was delayed by a 13-hour exposure as compared with a 10-hour exposure. As a rather extreme case reference is made to the behavior of wild sunflower as described on page 875. In this instance the unfolding of the flower buds was delayed for several months by the long daily light exposure.

As the light period is shifted away from the flowering optimum and toward the optimum for vegetative development one of the effects is cleistogamy. Thus, the sparse flowering of Mikania in spring, previously referred to, when the increasing day length is moving toward the optimum for vegetative activity, is usually associated with a cleistogamous type of blossom. The cleistogamous flower of the violet during the long summer days is to be regarded as a step away from the open, blue, colored blossom of spring and toward the purely vegetative form of development. These results are in line with observations of Bouché (*4*) on certain species, reported in 1875.

CHANGE FROM THE REPRODUCTIVE TO THE PURELY VEGETATIVE FORM OF ACTIVITY

It is of interest to inquire further into the effect of changing the plant from the optimal light exposure for sexual reproduction to one approximating the optimal for vegetative activity. If made in the earliest stages of development of the plant the change in light exposure would have little or no qualitative effect, while if made only after senescence has reached an advanced stage the only action of importance would necessarily involve rejuvenescence. This latter condition will be considered in later paragraphs.

Plantings of *Cosmos bipinnata* Cav. in 12-quart galvanized iron buckets germinated July 5, each bucket containing about a dozen seedlings. At the outset all plants were exposed to a 10-hour day, a light period which quickly forces flowering. Beginning July 6, one bucket of seedlings was transferred on each alternate day from the 10-hour day to the full daylight exposure of summer at Washington, D. C. All control plants remaining under the 10-hour day were showing flower buds on July 26. All plants transferred to the long-day conditions on or after July 18 likewise were showing flower buds on July 26, while the plants transferred during the period July 6 to 16, were showing no flower buds as late as September 2. It is evident that an exposure to a 10-hour day for not less than 10 days is necessary to bring the flower buds into evidence. The dates of first open blossoms ranged from August 9 for the plants remaining under the 10-hour day till July 26, to August 21 for those transferred to the long-day conditions on July 18. A notable feature was that of the numerous flower buds formed on the plants which were removed from the 10-hour light exposure on July 18 and July 20 only a few were able to open, the others being permanently suppressed, a result which has often been observed in cosmos and other plants. The foreshortening of the primary axis, with resultant crowding together of nodes, associated with the formation of the terminal flower bud, is followed by considerable swelling of the nodal tissues immediately beneath the bud as a result of the stimulus from the longer day. New

vegetative shoots encircling the flower buds soon begin to elongate, and the latter apparently is deprived of the necessary nutrition for development. It should be pointed out that in this experiment the formation of flower buds in all cases was associated with marked branching at the tops of the plants, while branching did not occur in those plants in which flower-bud formation was inhibited by the lengthened light exposure.

A similar experiment was undertaken with Biloxi soybeans. The seed, sown in 12-quart buckets, germinated July 2, and at the outset all seedlings were exposed to a 10-hour day. Beginning July 6 one lot of seedlings was transferred each succeeding day to permanent outdoor conditions, the last lot being transferred July 25. The results are shown in Table IV. The response to the change in the light period is similar to that of Cosmos. Here, again, 10 days' exposure to short-day conditions was the minimum for inducing flower formation. All plants thus responding also flowered again at the normal time for the variety in early fall as a result of the natural shortening of the day. It will be observed that although flowering was successfully accomplished where the soy beans were exposed to the 10-hour day for 10 to 20 days no fruits were developed, a fact which is regarded as important. Although the blossoms appeared to be normal it seems that under the influence of the long-day exposure even the stimulus of fertilization was not sufficient to permit development of the seed. Beginning with an exposure to the 10-hour daily light period for 11 days the fruits in increasing numbers were successfully developed.

TABLE IV.—*Effect of transferring Biloxi soybeans at intervals of one day from a 10-hour daily light exposure to the full daylight period of summer*

Date transferred to full daylight.	Date of opening of first blossom.	Date of second (normal) blossoming period.	Average height of plants.	Seed formation.
			Inches.	
July 6	Sept. 13	.....	42	No pods formed.
7	...do.....	.....	42	Do.
8	Sept. 14	.....	42	Do.
9	Sept. 13	.....	42	Do.
10	...do.....	.....	42	Do.
11	...do.....	.....	42	Do.
12	Aug. 9	Sept 15	42	No pods formed from first blossoms.
13	...do.....	Sept. 14	42	Do.
14	...do.....	...do.....	42	Do.
15	July 31	...do.....	40	Do.
16	...do.....	...do.....	40	Do.
17	...do.....	...do.....	40	Do.
18	...do.....	...do.....	40	Do.
19	July 27	...do.....	39	Do.
20	July 26	...do.....	38	Do.
21	...do.....	...do.....	36	Do.
22	...do.....	...do.....	36	Do.
23	...do.....	...do.....	35	A few pods formed from first blossoms.
24	...do.....	...do.....	32	Numerous pods formed from first blossoms.
25	...do.....	...do.....	28	Do.

SPRING FLOWERING AND FALL FLOWERING

The facts brought out in the preceding discussion of the relation between long-day and short-day plants and the balance between the vegetative and the reproductive types of activity throw light on the relationships existing between spring-flowering and fall-flowering plants. As is well known, many plants normally flower only during the spring, while many others regularly flower only in the fall. There are a number of plants, however, which flower in both spring and fall, although usually there is a marked difference in the extent of the flowering during the two seasons. Finally, there is a large group of plants which blossom in midsummer and a smaller group which under favorable conditions flower in winter. It is well known that in a very large number of perennials the flower buds are organized during the summer or early fall of the year preceding that in which the blossoms finally open, so that, in considering the effects of light duration, it is necessary to avoid confusing the action on the laying down of primordia and that on the final unfolding of the blossom.

Broadly speaking, in cool temperate regions short-day plants will flower chiefly in the fall rather than in the spring because of the lag in temperature rise in spring as compared with the lengthening of the day. In other words, in spring the day length is likely to become too long for flowering of short-day plants before the temperature has risen sufficiently to permit plants to become active. This is true more particularly of the annuals and those herbaceous perennials which require considerable vegetative development as an antecedent to flowering. That plants of these types which regularly flower in the fall will actually flower in the spring when the obstacle of low temperature is removed has been demonstrated in a number of cases. As a specific illustration Peking soybeans germinating in the greenhouse March 31 showed first open blossoms on May 12, or 42 days after appearance above ground, while a second lot germinating April 13, just two weeks later than the first planting, did not show open blossoms till July 16, 90 days after germination. Plantings of the Biloxi soybeans made on the same dates failed to flower till September, since the day length was already above the critical for flowering in this variety. The Biloxi quickly flowers, however, if planted in winter or early spring in the greenhouse. Indirectly, the many experiments already described in which various plants have been forced into flowering out of season by shortening the light period or inhibited from flowering in the normal season by increasing the light period furnish proof of this relationship of spring and fall flowering in the short-day plants. As the critical light period for flowering becomes longer the chances for spring flowering of the species are increased till finally spring flowering merges with summer flowering in those species which are intermediate between the more typical short-day and long-day plants. Again, sparse flowering in spring is to be looked for in those of the short-day plants which are able to flower at all, for the reason that the change in day length is toward the optimum for vegetative activity and away from the optimum for flowering. It is under these conditions, also, that various modifications and abnormalities in flowering and fruiting, quantitative as well as qualitative, are most likely to occur. On the other hand, the short-day plants as a whole will have their energies thrown into flowering and fruiting more or less quantita-

tively, as it were, through the change in day length in the fall when the change is away from the optimum for vegetative activity and toward the optimum for sexual reproduction. One importamt qualification must be made to this principle, namely, that it holds good only so long as the day length does not become too short for the flowering and fruiting processes.

The long-day plants, on the other hand, through late spring and early summer are subjected to a changing day length which is approaching the optimal for sexual reproduction, hence it is to be expected that these plants would flower and fruit abundantly during this period. A large proportion of spring flowering plants consists of woody and herbaceous perennials in which the flower primordia are organized during the summer preceding the spring in which the blossoms unfold. In this case it seems probable that the optimal day length for flower development following the summer solstice passes by before the embryonic flower buds have made much progress in their development and the direction of the change in day length through late summer and the fall is away from this optimum for flowering and fruiting and toward or through the optimum for vegetative activity. Under these conditions further development of the flower buds would be attended with difficulty so that their growth would be slow. If the onset of cold weather is delayed, some species may flower in the fall instead of in the normal spring season. In some, and probably in most instances, however, flowering would be inhibited by the short days of late fall and winter. On the other hand, the cold weather of winter may exercise a distinctly helpful influence on the completion of the flowering process by establishing a favorable balance of income over outgo. Consequently, the earliness of flowering in the spring will depend largely on how soon the temperature rises to the point where development can actively proceed. The necessary internal conditions for flowering having been established, it remains for rise in temperature in spring to speed up the unfolding of the blossoms. Nevertheless, the increasing length of the day in the spring undoubtedly remains a factor, particularly in those species which do not unfold their blossoms till spring is well advanced. This is seen, for example, in the case of the beet (p. 888).

APOGEOTROPISM, OR INCREASE IN STATURE

Apogeotropism or increase in stature is a response of great importance in photoperiodism; and, in ract, the experimental data thus far secured as a whole seem to indicate that in a sense this is the fundamental phenomenon underlying the various other responses, including flowering and fruiting, which are discussed in this paper. It appears that, in general, there is an optimal length of day for apogeotropic growth and any change to suboptimal conditions will result in checking the apogeotropic type of vegetative development, to be followed by various other forms of expression. With sufficient departure from the optimal light period the primary axis may be completely suppressed and aerial growth practically confined to leaf development, as typically shown in the leaf rosette of stemless plants. Another typical form of expression resulting from a rather extreme suboptimal light period is the prostrate or creeping habit of growth, stem elongation taking place without increase in stature. As the day length is advanced toward the optimum the rate of vertical elongation, as well as the final stature attained, are increased.

This relationship seems to hold whether or not flowering is involved and applies also to branches and leaf stems as well as to the primary axis. The seasonal length of day may be either too long or too short for maximal apogeotropic response.

It is probable that the first important result of departure from the optimal day length for apogeotropism is a foreshortening of the stem which results in, or at least is accompanied by, transformation of the terminal portion into an inflorescence. With a more marked departure from this optimum, such as would completely eliminate apogeotropic stem elongation, flowering gives way to leaf development. In other words, the foreshortening is pushed to the point where the terminal flower bud is replaced by the leaf rosette. This, at least, expresses the result morphologically even if it should have no physiological basis. As has been previously pointed out, many short-day plants of the type of Cosmos and Bidens continue for a more or less indefinite period vertical elongation of the axis under the influence of long days. As the day length is reduced to suboptimum, elongation of the axis is checked and flowering quickly follows. In these plants stem elongation can scarcely be completely eliminated by reducing the day length, and likewise flowering can not be readily inhibited by this means. In many long-day plants, on the other hand, apogeotropism may not be pushed so far as to inhibit the foreshortening and flowering, but by reducing the day length initial elongation of the axis is readily prevented. It is probable, moreover, that some of the woody perennials will be found to occupy an intermediate position in which more or less indefinite apogeotropic growth is induced by the optimal light period, on the one hand, and such growth completely inhibited, on the other hand, by suitable change of the light period to suboptimum.

A few examples illustrative of the above-mentioned responses will be of interest. In Comos, as stated on page 875, the axis reached a height of 15 feet under the influence of a long daily light exposure, and then flowering occurred only because of a decrease in the light period, whereas the final height attained under short-day conditions throughout was only 30 inches. Bidens, which behaves like Cosmos under long-day conditions, may attain a height of only 2 inches when exposed to a short-day length, the foreshortening of the axis being followed by flowering. It was pointed out, also, that while buckwheat flowers under all day lengths employed, under the longer light periods flowering is accompanied by marked increase in stature, the final height in this case being more or less indeterminate. Similarly, under an increase in duration of the light period from the normal day length of winter to about 18 hours, which was without effect on the time of flowering in Connecticut Broadleaf tobacco (*Nicotiana tabacum* L.), the height was increased by 50 per cent and the number of leaves was doubled. In the violet the leaf stalk is greatly lengthened by increase in the length of day. Goldenrod, as described on page 877 and illustrated in Plate 5, B, furnishes a striking example of inhibition of stem elongation by a reduced day length.

Summer radish (*Raphanus sativus* L.) when exposed to a daily light period of 7 hours is unable to develop a flowering stem, but under these conditions the leaves reach an unusually large size and the root continues to enlarge. Two plants which had received 7 hours of light daily during the preceding summer and fall were exposed to the natural day length of winter in the greenhouse till February 1. At that time it was seen that

in one of the individuals the increasing length of day had initiated development of a flowering stem. These plants were then restored to the 7-hour day length. In the plant which had begun the development of a stem, elongation of this stem was soon checked, the final height reached being only 24 inches (Pl. 3, A). This is in spite of the fact that the root had attained a diameter of nearly 5 inches. Final features of development in this interesting plant, as shown in Plate 3, B, will be considered under the subject of branching (p. 899). In spite of the large quantity of carbohydrate material stored in the root the height of the stem was sharply limited by the duration of the light period. The beet (*Beta vulgaris* L.) differs from the radish in that it usually behaves as a biennial and Klebs (*11, p. 292*) showed several years ago that this plant may be unable to flower the second season if kept in a warm greenhouse through the winter. Large roots which had been stored in an outdoor pit during the winter were set in soil and one lot placed under a 10-hour day on April 1. The control plants under natural day length flowered late in June as indicated in Plate *8*, B. Under the 10-hour light period elongation of the stems soon ceased and the apical buds developed into leaf rosettes. The 10-hour day was so far below the optimum for apogeotropic development that foreshortening apparently was too abrupt to permit of flowering. The final result of the short-day conditions was that aerial "beets" (thickened stems) were formed at the bases of the leaf rosettes. Referring back to the behavior of tropical sorghums (Table I), it may be noted that a day length of 13 hours approximates the optimum for apogeotropic response in some of these varieties, as for example in S. P. I. 43626. After the flowering stage had been reached the final heights under the 13-hour day were decidedly in excess of those under the full day length or the 10-hour day. The full day length evidently is excessive, while the 10-hour day is less favorable than the 13-hour day.

Preliminary observations on the growth of the apple (*Malus sylvestris* Mill) in contrast with that of *Acer negundo* L., for example, under different day lengths are of special interest. As will be seen by reference to Plate 4, B, seedlings of the latter are scarcely able to grow at all under a 10-hour day. In marked contrast, the apple grows more rapidly under a 10-hour day than under the full day length of midsummer. Young seedlings under the two light exposures are shown in Plate 4, A. Two specimens of standard Baldwin grafts and one of Baldwin grafted on a Paradise dwarf stock which were transplanted to large tubs in April and exposed to 12 hours of light daily soon began a rapid rate of growth which was maintained throughout the summer (Pl. 5, A). Of the three corresponding individuals similarly transplanted but exposed to the full daylight of late spring and summer, only the graft on Paradise stock survived, and up to August this grew much more slowly than the trees exposed to a 12-hour day. During August, however, it was seen that there was marked acceleration in the rate of growth of the control, continuing through early fall which, of course, is in line with the normal behavior of the apple. To arrive at the full significance of these results will require further study, but they seem to indicate that the long days of midsummer occurring in high latitudes are distinctly suboptimal for apogeotropic vegetative development in the case of the apple and therefore probably conducive to the initiation of flower-bud formation. As the tropics are approached the shorter length of the summer day would favor vegetative activity at the expense of flower-bud formation.

Similarly, since the general change from long to shorter days with the advent of late summer would favor vegetative activity, the growth and development of flower buds would be correspondingly retarded and, finally, cold weather, also, would operate to slow down both types of activity. Thus, the tendency would be toward sparse fruiting and rapid vegetative development with advance from high latitudes toward the equator; the shortening days of late summer would tend to delay final flowering till the following spring, particularly in high latitudes.

FORMATION OF BULBS, TUBERS, AND THICKENED ROOTS

Tuberization is one of the outstanding features of photoperiodism This fact is not so surprising, perhaps, in view of the significane of stem elongation as a fundamental factor in various responses of the plant to change in the daylight period. As is well known, tubers and bulbs represent extreme conditions of stem shortening accompanied by marked increase in diameter. Using the term tuberization in its broadest sense to include the formation of thickened roots as well as the more typical tubers, bulbs, and corms, the general feature of carbohydrate accumulation may be regarded as being common to all these storage organs. This accumulation obviously indicates an excess of carbohydrate over current consumption, but the important point to be emphasized in the present discussion is that the surplus of carbohydrate is not due to increased photosynthetic activity but rather inability on the part of the plant to utilize the carbohydrate, whether it be present in relatively large or small quantity.

As to the locus of the tuber or other storage organ it appears that the presence of previously formed buds or the ability to organize such structures is an important factor. Environmental conditions also play a part in determining the position of storage organs as well as in their formation. The work of Vöchting on this subject is of special importance. This investigator (*22*) showed that shoots of the potato (*Solanum tuberosum* L.) set in the soil in such manner that the underground portion consists only of an internodal section readily forms aerial tubers for the reason that the underground portion is incapable of developing adventitious buds. It was shown, also, that by suitably darkening the apex of the primary shoot on a branch the growing point is converted into a tuber and, consequently, it was concluded that darkeness favors tuber formation.

In later experiments with tubers of the Marjolin variety of potato taken from storage after having sprouted (*23*) Vöchting found that when germinated in darkness and with abundant moisture in soil and air roots and foliage shoots quickly developed but no new tubers were formed if the temperature was maintained at 25° to 27° C. With a temperature of 5° to 7°, on the other hand, no foliage shoots were formed, but instead numerous new tubers developed at the ends of old sprouts and new stolons and on the mother tuber. In other words, the growing points were tuberized. By transfer from the higher to the lower temperature the foliage shoots assumed horizontal direction of growth and formation of tubers began. Experiments with low partial pressures of oxygen indicated that decreased respiratory activity is not responsible for the low-temperature effect. It is important to observe, however, that germination in sand free from moisture gave no foliage shoots but only short roots and stolons bearing numerous tubers, regardless of whether the tem-

perature was high or low. By reducing the moisture supply after a foliage shoot some 10 to 12 cm. high had developed as a result of an abundant supply of moisture, further upward growth was stopped and numerous small aerial tubers soon formed. The picture thus presented (*23, Table IV, p. 114*) strongly calls to mind the general contour of a miniature shrub, defoliated but bearing numerous fruits. With moist soil but dry atmosphere the shoots which developed soon assumed a horizontal direction and numerous basal branches appeared. In germination tests in diffuse light a moist soil gave relatively large leaves and long internodes in the presence of moist air and short, thick internodes, mere scales rather than true leaves, and basal stolons in the presence of dry air. Tubers set upright in plates, without use of any soil, showed decreased elongation of the apical shoot with increased light intensity. Under these conditions light inhibited root formation.

In contrast with Vöchting's work on tuber formation, Bernard, in a lengthy article (*1*) dealing largely with the life history of the orchids, reached the conclusion that in many species a period of active differentiation is followed by a definite period of tuberization, while in other species tuberization begins in the earliest stages of development. In all cases Bernard found a close correlation between tuberization and infection with certain endophytic fungi and concluded that these parasites are the cause of tuber formation. This fungus theory of tuberization was extended to include the potato. It had been previously shown by Laurent (*12*), however, that shoots from potato tubers, which had been grown in darkness and were free from starch, developed tubercles in darkness when placed in saccharose solutions of proper concentration (10 to 20 per cent). Having subsequently confirmed these results Bernard (*2*) was forced to modify his views as to infection by fungi being the sole cause of tuberization. Molliard (*16*) showed that onion (*Allium cepa* L.) grown in a sterilized nutrient solution containing glucose is capable of forming a bulb and later (*17*) showed, also, that radish and certain other species form a starchy, thickened root under similar conditions. Thus, while it may be possible that in special cases tuberization is due to the invasion of fungi, it seems certain that parasitism or symbiosis is not the usual cause of the formation of tubers and other storage organs. Magrou, in a recent extended discussion (*15*), however, seeks to establish the importance of Bernard's fungal theory of tuberization.

"Sets" of the common Silverskin variety of onion were grown under different day lengths, 15 to 20 individuals being grown in each lot. In the first test the sets were planted in the greenhouse May 19. One lot was exposed to the natural day length while the second lot received in addition electric illumination of 3 to 5 foot-candles from sunset till midnight in the manner previously described. The summer temperature in the greenhouse was high, averaging 10° to 20° F. above the outside air temperature. The behavior of the plants both with and without artificial illumination was much the same as that of the outdoor controls except that the size of both tops and bulb was considerably reduced, as shown in Plate 9, A. The controls exposed to the full day length of summer developed in the usual manner. First blossoms opened July 14, large bulbs were formed, the tops died in due course, and there was no splitting into new individuals. The resting bulbs resumed vegetative development in September. A series exposed to 13 hours of light daily out of doors did not flower and the tops remained green throughout the summer.

The original bulbs in most instances gave rise to several new individuals, each of which eventually formed bulbs of considerable size. Under the full-day length only single stalks were formed, while under a 10-hour day each unit gave rise to several stalks. Under the 10-hour day there was permanent failure to form bulbs although the plants split into two or more new individuals. The appearance was that of spring onions, and the tops remained green for an indefinite period. Though the plants have remained green for more than 12 months there has never been any indication of flowering or bulb formation. With only 5 hours of light daily, weak shoots of pale green color developed and no bulbs were formed. A surprising fact is that flower buds were formed, though these were not able to open. This behavior possibly indicates that for plants of this type, having an intermediate length of day as optimum for vegetative growth, there may be two-day lengths favorable for flowering. The plants under the 5-hour day were short-lived. The effects of the exposures on formation of tops and bulbs are well shown in Plate 9, A. These results indicate that in the onion bulb formation as well as flowering and the resultant rest period are induced by the long days of summer while a shorter day length favors a period of vegetative activity of indefinite duration, thus eliminating bulb formation and the rest period which normally follows. The shorter day length does not interfere with the splitting into new units. The onion affords an instance in which the optimal day length for vegetative growth is relatively short while a long day results in dormancy following the development of a resting organ representing extreme shortening of the primary axis. Referring to Plate 9, A, it is interesting to note that the high temperature of the greenhouse greatly reduced the size of the plant as a whole but did not alter the general morphology. The addition of the electric light of very low intensity shows a slight attenuating effect, the plants being somewhat taller than those exposed only to natural daylight.

Tubers of the McCormick, a late variety of potato, were cut in the usual fashion and planted in the greenhouse May 21. One lot of the potatoes was exposed to natural daylight only while a second lot received, in addition, artificial illumination of 3 to 5 foot-candles from sunset till midnight in the manner previously described. As previously stated, the temperature in the greenhouse averaged 10° to 20° F. above the outside air temperature. In the house in which no artificial illumination was used the first blossoms opened July 3 when the plants were about 27 inches high. When harvested November 1 the average weight per plant of green tops and tubers combined was 1,127 gm. and that of the tubers alone was 340 gm. The average height of the plants was about 6 feet. The tubers were of small size. In the electrically lighted house flower buds formed, but none of them were able to unfold. When harvested November 1 the average height of the plants was 8½ feet and the average green weight was 1,528 gm. In this case no tubers whatever were formed, so that under the influence of the increased illumination period both sexual and vegetative forms of reproduction were suppressed. All energies of the plant were directed toward vegetative development. Tubers are resting organs, and the longer light period did not permit of slowing down in vegetative activity or any tendency toward dormancy. This is illustrated by the fact that an inderground bud which otherwise might have given rise to a tuber germinated and, in effect, developed an offset, the usual rest period of the tuber being eliminated (Pl. 8, A). Similar plantings of the McCormick variety also were made in boxes on

May 21 and were exposed to regulated day lengths by use of the dark houses. The exposures were 5, 10, 13 hours, and the full daylight period of the season. The plants were harvested August 28. The results of the test are summarized in part in Table V. The conditions in general and the soil in particular were unfavorable for the best development of tubers, but for comparative purposes the results are of considerable interest.

TABLE V.—*Results with McCormick variety of potato exposed to different daily light periods*

Duration of daily light period.	Date of first blossom.	Average height when harvested.	Average weight of tubers.	Average weight of tops, air-dried.	Ratio of tubers to air-dried tops.	Condition of tops when harvested.
		Inches.	*Gm.*	*Gm.*		
5 hours	July 2	20	80	2.8	12.1	All dead.
10 hours	do	12	320	1.9	168.1	Mostly dead.
13 hours	do	25	664	30.9	22.1	Green.
Full daylight period	July 23	32	471	32.0	15.1	Do.

With exposures of 5 and 10 hours of light daily the blossoms unfolded but no seed balls were formed. Taking the two experiments together it appears that a very long daylight period tends to direct the activities of the plant toward vegetative development to the exclusion of other alternative forms of expression. With a somewhat shorter daylight period the tendency is toward successful sexual reproduction and moderate tuber formation. With further shortening of the daylight period seed development again fails and there is a tendency toward tuber formation to the exclusion, as far as may be, of other alternative types of expression. Finally, with an extremely short daylight period it is seen that there is some tendency toward return to exclusive vegetative development. With a light duration of 10 hours or thereabouts there is a condition of intense tuber formation; in other words, there is an optimal light duration for tuberization as well as for flowering and fruiting and for purely vegetative development. Since one of the limiting factors in tuber formation is the quantity of photosynthetic material formed, the actual or absolute weight of tubers is greatest under a somewhat longer daylight period, namely 13 hours. Under natural conditions, however, the seasonal range in day length becomes an important factor; and it may well be that in northern latitudes the long days of summer leading to extensive foliage development, followed in autumn by a correspondingly precipitate decline in day length, constitute a very favorable situation for tuber development. It may be added that nothing in this discussion should be construed as minimizing the significance of relatively low temperatures in tuber development, particularly with respect to size of tuber.

Tubers of ground nut (*Apios tuberosa* Moench) planted in boxes in the greenhouse early in March germinated April 6. Beginning April 20, one lot was exposed to 10 hours of light daily while a second lot was exposed to the full seasonal day length. Flower buds were showing on both lots when the light treatment began. On the control plants exposed to the full-day length the first open blossoms appeared June 1, and these plants were in full bloom till late in August. Under 10 hours of light

daily only 1 or 2 blossoms opened on each plant, the remaining flower buds being suppressed. The leaves assumed a dark green color, growth of the vines ceased and above ground the general appearance was suggestive of a sort of dormancy. In September both lots of plants died back to the ground level. The underground portions were harvested October 28. The control plants had produced a network of small tubers throughout the soil of the boxes, but the mother tubers had enlarged but little and their resting buds were small. The plants exposed to a 10-hour day, on the other hand, had enlarged the mother tubers to several times their original size, and they bore a large number of prominent resting buds but only a very few new tubers were formed. The new tubers, however, were noticeably larger than those formed under the full day length. The total weights of all tubers under the long-day and short-day conditions were 625 and 383 gm., respectively. These results are of special interest in bringing out the difference in mere enlargement of a storage organ, on the one hand, and the organization of new units, on the other hand. Apparently under the shortened illumination period there was a dearth of some formative material other than storage forms of carbohydrate. The original or mother tubers when grown a second season under a 10-hour day continued to enlarge as in the first season, attaining an average weight of 7½ ounces. It is of interest to note that the behavior under the 10-hour day closely approaches that of the related species *Apios priceana* Robinson, occurring in Kentucky. Under the natural day length of summer the latter species forms only a single tuber, which attains large size.

A bean from South America (*Phaseolus multiflorus* Willd). planted May 13, was exposed to regulated day lengths beginning June 3. Under the full day length of summer only moderate growth was made and there was no flowering. In October these plants were transferred to the greenhouse, electrically illuminated from sunset till midnight, and under these conditions growth was more vigorous than in summer but there was no flowering. Under a 12-hour day the plants behaved much like the preceding controls and there was no flowering. These plants were transferred to the greenhouse not provided with electric lights October 15. A few blossoms appeared November 29 and two seed pods matured. Under a 10-hour day flower buds were showing by July 15 and a number of blossoms opened, though no seed developed. Sparse flowering again occurred in September and in November. The plants were transferred to the greenhouse in October with the 12-hour day plants. The plants of the three series were taken up and photographed January 18. As shown in Plate 6, A and B, the roots of the plants exposed to 10 hours of light in summer and the short day length of winter were strongly tuberized, while under the long day length of summer and the artificially lengthened daylight period of winter there was no tuberization at all. The plants exposed to a 12-hour day in summer and the natural day length of winter showed only moderate tuberization of the roots. Without going into details it may be stated, also, that cuttings of two varieties of dahlia made May 10 were grown during the summer months in the greenhouse with and without electric illumination at night. Under the lengthened illumination period there was almost complete elimination of the usual formation of tubers.

Cinnamon vine, *Dioscorea divaricata* L., was grown under regulated day lengths, both from aerial tubers and from 1-year-old underground

tubers. The details of the experiments are summarized in part in Table VI. All plantings were harvested September 26. Cinnamon vine, like Peking soybeans, responds very promptly to the decrease in length of day beginning with the summer solstice, only that the response takes the form of tuberization of aerial axillary buds instead of flowering. Under the natural length of day the aerial tubers appear one month after the summer solstice, and this holds true for the progenies of both the aerial and the larger subterranean tubers. By exposure to an artificially shortened day length of 13 hours or less, beginning at the summer solstice, the appearance of aerial tubers was hastened by about two weeks. As is to be expected from the quick response to the first shortening of the day length following the summer solstice, the maximum effect in hastening the aerial tuberization is produced by a 13-hour day, further reduction in day length to 12, 11, or 10 hours being without effect. By exposing the plants to the reduced daily illumination period earlier in the season the date of appearance of aerial tubers is advanced accordingly. When the treatment is applied in the earlier stages of development, however, a longer period of time is required for the tubers to come into evidence than when considerable advance growth has been made. In all cases growth of the vine is quickly checked by exposure to the reduced day length. The effect is so pronounced that exposure to a length of day of 11 hours or less causes dying back of the young tips of the vines. This dying back practically ceases with a day length of 12 hours. It was not practical to obtain actual weights of aerial tubers produced under the different conditions of illumination, but it was observed that these tubers were formed in greatest number and of largest size under the 10-hour and 11-hour daily light exposure. Under a light period of 12 hours or more there was increasing tendency toward continued vegetative growth and reduced production of aerial tubers. There seem to be no marked, consistent differences in ratio between the weights of underground tubers and vines under the various light exposures. The underground tubers produced larger vines than the aerial tubers under the shorter light periods.

TABLE VI.—*Effect of differences in length of day on tuberization in cinnamon vine*

Kind of tubers planted.	Number of plants grown.	Date of germination.	Date of beginning light treatment.	Length of day to which exposed.	Date of first appearance of aerial tubers.	Average weight of tubers and vines.	Average weight of green vines.	Average weight of tubers.	Ratio of tubers to vines.
						Ounces.	*Ounces.*	*Ounces.*	
Aerial	1	Mar. 22	May 2	8 hours	June 20	4	1½	3½	7:1
Do	3	...do	...do	10 hours	...do	10	1	9	9:1
Do	1	...do	June 21	...do	July 4	6	2	4	2:1
Do	2	...do	July 23	11 hours	July 3	11½	3	8½	2.8:1
Do	1	...do	June 21	...do	July 2	6½	1½	5	3.3:1
Do	1	...do	...do	12 hours	July 7	3½	1	2½	2.5:1
Do	1	...do	...do	13 hours	July 2	4½	1	3½	3.5:1
Do	5	...do	Controls.	Full day length.	July 21	16	4	12	3:1
1-year-old underground.	1	Apr. 27	Mar. 22	8 hours	June 15	5½	1½	4	2.7:1
Do	1	Apr. 26	July 23	...do	July 22	19	9	10	1.1:1
Do	1	Apr. 27	Mar. 22	10 hours	June 23	8	2	6	3:1
Do	1	Apr. 21	June 21	...do	July 2	21½	8½	13	1.5:1
Do	1	Apr. 26	...do	11 hours	July 8	17	7	10	1.4:1
Do	1	May 4	...do	12 hours	...do	19½	3½	16	4.6:1
Do	1	Apr. 25	...do	13 hours	June 30	18½	4½	14	3.1:1
Do	3	Apr. 26 to May 29.	Controls.	Full day length.	July 21 to 23.	18½	7	11½	1.7:1

Tests were made with two varieties of yam (*Dioscorea alata* L.) furnished by the office of Foreign Seed and Plant Introduction, Bureau of Plant Industry. In each case two plants were grown in a box 3 feet long, 10 inches wide, and 10 inches deep. For plantings of the variety S. P. I. 46801 small root tubers were used, and for the variety S. P. I. 47001 aerial tubers were employed. All plantings were made May 14 and all tubers germinated between May 23 and June 4. The different light exposures began at time of planting. The yams were harvested October 6. Under a day length of 10 hours the yam S. P. I. 46801 developed at first a very marked chlorosis, the leaves taking on an almost pure yellow color, but by June 25 there had been a decided change toward the normal green. None of the plantings of either yam flowered in these tests. The variety S. P. I. 46801 formed no aerial tubers under the 10-hour exposure, but with 12 hours of light daily and under the full day length these tubers appeared. The variety S. P. I. 47001 formed no aerial tubers in any case. The relative development of vines and underground tubers under the different conditions are shown in Table VII.

TABLE VII.—*Behavior of two varieties of tropical yam under daily illumination periods of different duration*

Duration of illumination period.	Combined weights of vines and tubers.	Weight of tubers.	Weight of vines.	Percentage of tubers.
S. P. I. No. 47001:	*Ounces.*	*Ounces.*	*Ounces.*	
12 hours	126	81½	44½	64.7
Control; full day length	81	11½	69½	14.1
Do	79	11	68	13.9
Do	67	9	58	13.4
S. P. I. No. 46801:				
10 hours	117	86½	30½	73.9
12 hours	117	88	29	75.2
Control; full day length	109	41	68	37.6
Do	91	39	52	42.8
Do	106	55½	50½	52.3

It is quite clear that the shortened length of day caused a pronounced increase in tuber formation. The relative sizes of tubers formed by variety S. P. I. 47001 under a 12-hour day and the full summer day length are shown in Plate 10, A. It should be mentioned that while the plants exposed to the shorter day lengths formed only single thickened roots the controls tended to form more than one thickened root each.

Tubers of artichoke, *Helianthus tuberosus* L., were planted April 25 and were up May 5. Under a 10-hour day flower buds could be seen by June 21. The first evidence of flowering was a branching of the stem followed by formation of the flower buds. These buds, however, never developed to the flowering stage and by July 28 had been absorbed. By August 15 the plants were dead, having reached a height of about 2 feet. On the two control plants flower buds were showing August 30, and on one plant the first open blossoms were seen on September 22, while on the second plant the blossoms had not opened on October 1, when all plantings were harvested. Under the 10-hour day the plants

were small and appeared weak at all stages, but the two individuals together formed 35 tubers weighing 2 pounds and 4 ounces. Of the two controls, one reached 6 feet in height and the second 3 feet. The total number of tubers was 60, but these weighed only 1 pound and 1 ounce. Under the short-day exposure tuberization might be said to have been complete; that is, there were no elongated underground stems. As already stated, flowering could not be successfully accomplished so that there was no diversion of formative material toward seed formation. Under the natural range in length of day, on the other hand, there were many long underground stems with nodes only slightly tuberized, and in some instances no thickening of nodes at all could be seen. The tubers formed under the two conditions were strikingly different in appearance, as can be seen in Plate 7, A and B.

In the second series of tests with blazing star previously described (p. 876), it was observed that under the shortened daily light exposures well-developed corms of considerable size were formed, while the control plants, though many times larger in size, formed small corms or none at all.

Under the influence of a day length shortened to the point where successful flowering and fruiting is almost completely inhibited even the nodes of both primary and secondary stems of soybeans may be partially tuberized, as is shown in Plate 9, B. The arrested development of the flower buds accompanying the thickening of the stem is plainly seen.

The behavior of radish and beet under different day lengths has already been rather fully discussed (p. 887), and it only remains to point out here that under a short daily illumination period these plants continue to store up carbohydrate for a more or less indefinite period, eventually forming enormously thickened roots but no primary stem.

SIGNIFICANCE OF TUBERIZATION AS A FEATURE OF PHOTOPERIODISM

The data which have been presented will suffice to show that the prevailing length of day is an important factor in the formation of bulbs and tubers, as well as in flowering and fruiting. These data clearly indicate that the length of day not only influences the quantity of photosynthetic material formed but also may determine the use which the plant can make of this material. Under the optimal illumination period for apogeotropic development there is normally no accumulation of unused carbohydrate, this material being utilized as rapidly as formed in the development of structures or tissues incident to maximum increase in stature. Under these particular conditions it may well be that the quantity of carbohydrate produced is a chief limiting factor in rate and extent of stem elongation. Any departure from this optimal light period will check stem elongation; and the first outstanding result is initiation of flowering; that is, the growing point is transformed into an inflorescence. The natural result of checking stem elongation is a tendency toward accumulation of carbohydrate. In successful fruiting this carbohydrate (in many cases first converted into oil) is stored in the seed and its coverings. Thus, in a special sense, the seed may be regarded as a tuberized structure. From the standpoint of nutrition, apparently one of the functions of fertilization as a prerequisite for successful setting of the fruit is to aid in setting up a "center of attraction" about which nutrient materials will be mobilized. Since there may be an optimal

light period for sexual reproduction which tends to direct the energies of the plant quantitatively toward flowering and fruiting (see p. 881), it seems possible that in some species exposure to this optimal light period will be found to favor successful fruiting without the aid of fertilization. In other words, the duration of the light period may be a factor in parthenogenesis and in the development of seedless fruits.

As the length of day is removed still further from the optimum for stem elongation, flowering and fruiting tend to give way to formation of the usual forms of vegetative reproductive structures in which tuberization is a characteristic feature. Tuberization marks a further step toward complete elimination of stem elongation. There is no hard and fast line between flowering and fruiting, on the one hand, and formation of tuberized vegetative reproductive structures on the other; and an intermediate day length may permit of both types of development just as vegetative stem elongation and sexual reproduction may proceed simultaneously. Various steps in the complete separation between sexual reproduction and the formation of tubers, however, are readily traced in the experimental data which have been given. In the soybean a sufficiently reduced light period which marks the end of successful flowering and fruiting likewise marks the beginning of tuberization in the stem. With Irish potato a daily light period of 18 hours caused vegetative development almost exclusively, for, although flower buds appeared, they were unable to unfold, and tuber formation was completely inhibited. Under the natural seasonal day length of 14 to 15 hours the plants flowered freely and there was moderate tuber formation. With 13 hours of light there was a decided increase in quantity of tubers formed, while with 10 hours of light there was very intense tuber formation, the ratio of tubers to "tops" being increased sevenfold as compared with the plants exposed to a light period of 13 hours. With a light period of only 5 hours there was a sharp decline in the ratio of tubers to tops, indicating, perhaps, that the income of carbohydrate by photosynthesis was but little in excess of immediate requirements for the limited growth which the plant could make. The results obtained with *Apios tuberosa* and with *Helianthus tuberosus* show, also, that the type of tuber formed may be markedly affected by the duration of the light period.

Associated with the change from flowering and fruiting to tuber formation there is a tendency toward the transfer of growth activity from aerial to underground parts of the plant. Thus, underground tuber-forming stems tend to replace aerial flowering stems. As the light period is further shortened even the elongation of underground stems is checked, with the result that the number of tuberized reproductive structures is reduced while their size is correspondingly increased. The final stage is reached in those cases in which tuberization is confined to the mother stem, as in the beet and radish when exposed to the action of a light period of short duration. In this case stem shortening has been pushed to the limit and the plant consists essentially of a rosette of leaves connected with the root system by means of an enormously thickened stem entirely lacking in power to elongate or to form aerial or subterranean branches.

The available data indicate that there is an optimal light period for tuber formation just as there are optimal periods for stem elongation and for sexual reproduction. The highest proportionate production

of tubers occurs with a light period which admits of only very limited stem growth. The absolute maximum production of tubers, however, is obtained with an intermediate light period, or, as actually occurs each year in higher latitudes, with a light period favorable to extensive stem growth followed by a period favorable to intensive tuber formation. In all cases thus far studied typical tuber formation takes place as a result of decrease of the daily light period below the optimum for stem elongation so that this type of tuberization is greatly favored by the shortening of the day in fall following the long summer days of high latitudes. Bulb formation, as illustrated by the onion, on the other hand, takes place as the result of increase of the daily light period above the optimum for stem growth so that formation of these structures is favored by the long days of summer which occur in high latitudes.

The results of the experiments in tuberization seem to show that the remarkable regulatory action of change in the length of day on stem elongation and various associated phenomena cannot be due directly to change in the quantity of carbohydrate formed through photosynthesis. The content of plastic carbohydrate in the plant at any given time, of course, will depend on the relation between rate of formation through photosynthesis and the rate of consumption in promoting growth and other vital functions. Tuberization furnishes visible evidence that under the prevailing conditions production of total carbohydrate is in excess of current consumption except in so far as local tuberization may be the result of mere transfer of preformed storage material from other parts of the plant. There seems to be little doubt but, beginning with the optimal day length for stem growth, decrease in length of day in general involves decreased formation of carbohydrate. It appears, however, that progressive loss of power to grow as a result of decreasing day length advances more rapidly than would be required from the decreased formation of carbohydrate as a controlling factor. It is necessary, therefore, to conclude that the duration of the light period exercises a regulatory action on internal processes of the plant other than those which merely determine the total quantity of carbohydrate produced. It remains to be determined whether the additional action is to regulate the form of carbohydrate produced or to control other processes not so clearly connected with carbohydrate formation. In any event there is convincing evidence that the duration of the daily light period is an important, and often a controlling, factor in determining whether the plant may use the product of photosynthesis as rapidly as elaborated in promoting growth or, instead, must store the material, perhaps for its own subsequent use or for the nutrition of its sexually or vegetatively produced progeny.

CHARACTER AND EXTENT OF BRANCHING

One of the characteristic effects of altering the light period from optimum to suboptimum for apogeotropic response is to promote branching. This increased tendency toward branching is frequently associated with flowering, a fact which is not surprising since both are promoted by a change in the same direction in the duration of the light period. Branching and flowering are not always associated, however, for not merely the direction but also the extent of the change in the light period must be taken into account. Apparently the most favorable light period for aerial branching lies between the apogeotropic optimum and that

period which is so far removed from the optimum as to permit only the leaf-rosette type of development, with complete inhibition of vertical elongation of the stem. Moreover, both the character and the extent of the branching appear to be influenced by the seasonal range in length of day.

Under the influence of long days cosmos continues to elongate the major axis, more commonly with no branching and even with a minimum of leaf development. Shortening the day length sufficiently to induce flowering also invariably causes branching at the top of the plant, as in the experiment discussed on page 883. In Table II data are given on the extent of stooling noted in the small grains. It is clear that in the spring types of wheat, rye, and barley stooling was greatly increased under the relatively short, natural day length of winter as compared with the artificially lengthened light period. This condition is reversed in the winter wheat and rye. This difference in response doubtless depends on fundamental differences in light requirements between the winter and the spring types of the small grains. The Honey variety of sorghum was sowed May 21 in the greenhouse. Under the natural day length of summer the plants began shedding pollen August 19, and as the days shortened there was marked stooling, many of the new basal shoots attaining the height of the original stem. A similar lot of plants receiving electric light from sunset till midnight began shedding pollen August 6. In this case the branching was confined chiefly to the tops of the plants, a behavior resembling that of cosmos. These differences in habit of branching are shown in Plate 11, A and B.

Rosettes of *Oenothera biennis* L., transplanted and placed under a 10-hour day beginning March 29, showed marked basal branching while the controls exposed to full daylight developed only a primary axis. This difference in behavior is shown in Plate 12, A. In the earlier stages the basal branches showed a prostrate type of growth but eventually showed a decided apogeotropic form of growth, as may be seen in the illustration. Returning to the final stages of development of the radish plant which had been long maintained under short-day conditions, as described on page 888, the influence of the short-light period on the growth of the branches is striking. Ordinarily the flowering stem of the radish branches chiefly at the top, as did the present plant at the outset. (Pl. 3, A.) As a result of the shortened day length to which it had been recently transferred the basal branches gained the ascendency and the plant gradually assumed the general shape and the type of branching of a shrub. The light-darkness ratio was such that the accumulated nutrient material could be used only for forms of growth involving a minimum of apogeotropic response. Finally, the pendent form of elongation of the primary and secondary stems assumed unusual prominence, producing a sort of "weeping-willow" effect, and marking the last phase of development. Apparently, there was at the end almost complete loss of the power for apogeotropic development. (Pl. 3, B.)

The duration of the daily light period also is a factor in the elongation of underground stems. As stated on page 876, Rumex is unable to develop flowering stems when exposed to a short day length. Aerial development is limited to the formation of leaf rosettes, as shown in Plate 12, B. In this case, however, there is very active underground development of stems, indicating, perhaps, a further step toward complete loss of the power of growth against the force of gravity. It may be surmised,

therefore, that the length of day is a factor in the so-called "law of level" applied to underground stems. Thus, in effect, a change in day length from optimum to suboptimum for apogeotropic stem elongation may cause the apical bud to lose its dominance and lateral buds to become active. As stages in the response to departure from the optimum light exposure for increase in stature may be noted branching at the top, middle, or base of the aerial portion of the axis; various degrees of erectness in the resulting branches, from the upright to the pendent form; the prostrate or creeping form of stem elongation; and development only of the underground type of stem which, in turn, may change its direction of growth upward or downward with a change in the daylight period toward or away from the optimum for negative geotropism.

ROOT GROWTH

Preliminary observations indicate that the duration of the daily illumination period may exert a marked effect on the relative development of the root and the aerial portions of the plant. For example, a cutting of Biloxi soybeans made no top growth at all through the winter months and the original leaves assumed a very dark color and generally unthrifty appearance. Apparently new buds were unable to develop. Upon examination of the underground portion of the plant in the spring it was seen that the soil contained a large mass of roots altogether out of proportion to the top of the plant, as judged by the usual summer growth. Other similar cases have been observed in which a light duration unfavorable to aerial development has caused extensive root growth. Growth of root and shoot, therefore, are not necessarily contemporaneous with respect to season, and arrested development of the exposed portion of the plant caused by suboptimal light duration need not be accompanied by checking of root growth.

PUBESCENCE

A feature of the experiments with *Amaranthus hybridus* L. described on page 873 worthy of note is the fact that under the shortened light exposures of 5, 10, 12, and 13 hours daily the leaves were glabrous and the veins were not prominent. The leaves of the control plants, exposed to the full-day length, on the other hand, were noticeably pubescent and the veins were decidedly more prominent.

Specimens of wild lettuce (*Lactuca spicata* (Lam.) Hitchc.) were transplanted to boxes from the field March 29 when in the form of small rosettes. Under a 10-hour day the first blossoms opened August 24, and under the full summer length of day the first blossoms opened August 21. The average heights were 65 and 96 inches, respectively. Under the shortened light exposure the reduction in stem elongation was accompanied by a marked increase in the size and in coarseness in texture of the leaves, as shown in Plate 10, B. There was, also, a striking increase in the pubescence and roughness of the leaves and stem under the short daylight exposure.

Thus, in the case of the short-day plant Amaranthus pubescence was not favored by shortening the light period, but in the case of the long-day plant Lactuca the shortened daylight period was markedly effective in this respect.

PHYSIOLOGICAL TRANSLOCATION

As was brought out in the preceding discussion of apogeotropism and of branching, a day length sufficiently below the optimum for apogeotropic expression often results in the leaf-rosette type of development (or prostrate form of stem growth), with more or less complete inhibition of upright stem elongation. Again, where upright growth of the primary axis has already taken place a change to suboptimum in the light duration tends to break down the dominance of the apical bud over the lateral buds, thus causing development of either aerial or subterranean secondary stems or branches, depending on the species in question and on the extent of the change in light duration. A third important phase of apogeotropism now requires consideration. Under the influence of the apogeotropic stimulus the lower parts of the plant, including leaf, stem, tuber, and thickened root, may yield up their nutritive constituents to the upper plant parts and for the most part tend to pass into a state of senescence, often followed by death. Thus, under the influence of a favorable light exposure the plant in increasing its stature may use over and over again, within limits, elements of plant food which may be available only in limited quantities. Conversely, under an unfavorable light duration the movement of plastic nutrient material is downward rather than upward, with resultant increased growth of the lower plant parts (branching, stooling, stolon formation, development of rootstocks, growth of roots, etc.) or, with a still less favorable light duration, formation of underground storage and resting organs. With only a moderate departure from the optimal light duration for increase in stature the effect may be to initiate flowering. In this case translocation toward the apex is not interrupted unless the change in the illumination period is too great. In the latter event the movement of food materials is diverted downward and successful fruiting is prevented, as, for example, in poinsettia exposed to a 10-hour day (see p. 876).

In a recent investigation Schertz (*21*) concluded that mottling of the older leaves of *Coleus blumei* is due to a failing nitrogen supply. There can be no doubt of the fact that with only a limited supply of nitrogen available there is often a decided tendency for the lower leaves to yellow and wither, while the upper portion of the plant continues to grow. For example, it is well known by tobacco growers that too low a proportion of nitrogen to phosphorous in the soil will cause "firing" or dying of the lower leaves of the tobacco plant. It still remains, however, to explain why the lower, more mature leaves yield their nutrient materials to the upper portion of the plant when the available supply of these nutrients is limited. It seems reasonable to suppose that this phenomenon is largely a manifestation of apogeotropism, and it appears that appropriate duration of the daily illumination period is a controlling external cause of this manifestation, whatever may be the internal mechanism through which it operates.

Thus, when exposed to a long day Cosmos has attained a stature and size out of proportion to the small volume of soil supporting the root system in the container. Under these conditions, however, the lower leaves soon perish so that only a comparatively narrow zone of living foliage immediately beneath the growing part follows the upward growth of the stem. In similar manner the lower portions of the stem tend to become woody and retain only minimal quantities of the plant food elements needed by the upper growing portion. The conclusion that

under the long-day influence there is active upward movement of nutrients from the lower portion of the plant seems to be supported by the fact that cutting back the stem quickly results in a swelling of the upper residual node, followed by rapid growth of branches (Pl. 17, A), an effect which is not observable under short-day conditions. Poinsettia shows even more markedly than Cosmos this tendency to continue upward elongation of the stem under the long-day stimulus in spite of a limited supply of nutrients from the soil, and, in doing so, to constantly shed the lower leaves as stem growth proceeds (Pl. 19, B).

For successful fruiting, after flowering has been initiated, it is essential, of course, that the reproductive structure receive from other plant parts an adequate supply of food materials. It is apparent that ordinarily such a supply of nutrients is assured under a day length approximating the optimum for initiating flowering. Under a length of day veering toward the optimum for apogeotropic response the direction of the food stream is not changed but the tendency is for diversion of the arriving food material to the development of vegetative structures, thus causing shedding of the blossoms or young fruit. A change in length of day in the opposite direction, however, if sufficiently marked will tend to direct the food stream downward, thus favoring the development of lower branches, leaves, bulbs, tubers, and roots. In some cases there appears to be an intermediate condition in which the food stream still moves to the upper parts (or is arrested before passing downward), but the light relations will permit neither vegetative nor floral buds to grow. Under these conditions aerial tubers may result, or in perennials the food material is simply deposited in the stem in the region of resting buds.

PIGMENT FORMATION

It is well known that continuous exposure to darkness for considerable periods of time ordinarily leads to etiolation. According to Bonnier (*3*) continuous exposure to electric illumination of an intensity much lower than that of sunlight causes a much greater development of chloroplasts and formation of chlorophyll than under normal conditions. In view of these facts the effects of differences in the length of the daily illumination period are striking. Exposure to a very short day length commonly leads to well-defined etiolation, but in some cases there is, after a time, more or less complete recovery, the tendency being toward a return to the normal green color. Under a 5-hour day turnip (*Brassica rapa* L.) became extremely etiolated and died after attaining a height of only a few inches. On the other hand, peanut (*Arachis hypogoea* L.) under similar conditions showed only slight evidence of etiolation at first and, soon becoming noticeably greener, made comparatively good growth throughout the summer. Sweet potato (*Ipomoea batatas* L.) became severely etiolated but later partially recovered and made fair growth. Soybeans behaved much the same as sweet potato. Irish potato showed severe etiolation and made relatively poor growth. *Aster linariifolius* L. retained its green color throughout. Under a 10-hour day *Dioscorea batatas* L. became markedly etiolated but subsequently almost completely recovered its normal green color.

In striking contrast with these etiolation effects, exposure to a length of day in excess of that producing etiolation but still below the optimum for flowering usually causes the leaves of the plant to assume a shade of green much darker than the normal. This effect has been noted in a

large number of species. While in a number of species there is a decided tendency toward eventual recovery from the condition of etiolation caused by a light exposure of very short duration, the reversed condition of increased depth of green color induced by a somewhat longer light exposure appears to be permanent so long as the proper light conditions prevail. This dark green color is associated with a condition of relative inactivity in the green portion of the plant so far as appearance goes, for typically there is little or no growth above ground. There is usually intense activity underground in this case in the formation and development of underground stems, tubers, and roots.

It is hardly necessary to discuss at length the fact that the changes in color of foliage leaves which are regularly associated with autumn leaf fall may follow in a natural manner as a sequel to flowering, fruiting, and other phenomena leading up to senescence, dormancy, or death of the plant when these processes are developed through artificial control of the light period. It will suffice, perhaps, to give a single, very interesting case illustrating the fact that color changes affected by the light duration are not confined to the chlorophyll pigments. A specimen of poinsettia forced into flowering by exposure to a 10-hour day, which was accompanied by the usual rich coloration of the bracts of the inflorescence, as described on page 876, was transferred September 2 to the greenhouse electrically illuminated from sunset till midnight. Under the influence of the lengthened illumination period a tendency toward replacement of the red color of the bracts by chlorophyll green soon became evident. The bracts persisted for many weeks, the younger ones assuming a clear green color. Finally, in December vegetative growth was resumed at the extreme tip of the inflorescence. The first growth of the new shoot was of the weak, pendent type, and the stem was red in color instead of the normal green. Eventually, however, the stem assumed upright growth and developed the usual green color. These color relations are well shown in Plate 1.

ABSCISSION AND LEAF FALL

In the case of such annuals as regularly shed their leaves before dying abundant evidence already has been given of abscission and leaf fall as phenomena following flowering and fruiting induced by suitable regulation of the length of day. Soybeans furnish a good example. Under the proper length of day flowering and fruiting are promptly followed by yellowing of the leaves, which take on a rich golden yellow color. Abscission is soon completed and, as a result, the stalks are practically bare of leaves when final maturity is reached. These effects are clearly shown in the previous article (7, *Pl. 66 and 69*).

Specimens of smooth sumac (*Rhus glabra* L.) were transplanted to wooden boxes in April and allowed to grow under outdoor conditions during the summer. On September 8 one lot was transferred to the greenhouse electrically illuminated from sunset till midnight while the second lot was placed in the greenhouse receiving natural light only. Under the latter conditions the leaves soon colored, although leaf fall was slightly delayed and the colors were not as bright as normal for the species. Under the lengthened illumination period there was no autumn coloration or falling of leaves. With the added electric illumination of very low intensity no additional top growth took place, but the leaves assumed an abnormally dark green color which was retained

through the winter. Although resting buds had been organized at the bases of the leaf petioles, these did not develop, and the general appearance above ground was one of comparative inactivity. Eventually, however, new shoots emerged from the soil as offsets. It is apparent that the light conditions were such as to permit of limited vegetative activity, thus preventing leaf fall, but these conditions were unfavorable for strong apogeotropic response. The appearance of the plants in January under natural winter illumination only and with the added electric illumination is shown in Plate 13, A and B.

Similar tests were made with dwarf sumac (*Rhus copallina* L.). Under natural illumination only, the leaves were only slightly delayed in coloring and falling, the colors being somewhat less intense than usual, and the plants did not awaken from dormancy during the winter. With the addition of the weak electric illumination, coloring and falling of the leaves was delayed for several weeks, although eventually the leaves were shed and the plants became dormant.

Experiments were carried out with the tulip tree (*Liriodendron tulipfera* (L.) in a similar manner. In this case transfer to the electrically illuminated greenhouse in September was promptly followed by renewal of active growth of aerial parts with abundant development of new leaves. There was no definite period of leaf fall, only individual older leaves gradually dying back. There was no abscission, and even after the leaves were dead the petioles remained firmly attached to the stem. In this manner the plants continued active vegetative development till the experiment was discontinued at the end of 18 months without having shown any indication of abscission or definite period of shedding of the leaves. The control plants soon lost their leaves through abscisson and remained dormant through the winter. The appearance of the plants under the two conditions of illumination is shown in Plate 14, A and B.

Thus, in the three species considered it is seen that weak electric light (3 to 5 foot-candles) as a supplement to the sunlight of short winter days has ranged in effectiveness from simply delaying leaf fall to causing more or less complete resumption of normal vegetative activities.

In the foregoing experiments it is shown that natural shortening of the day length in fall and winter results in leaf fall through abscission. It is not to be inferred from these results, however, that abrupt change from a long to a very short day will accomplish the same result. It already has been pointed out (p. 902) that in a large class of plants exposure to an illumination period slightly longer than that causing etiolation leads to development of an abnormally dark green color in the leaves. Under these conditions flowering occurs with difficulty or not at all and visible evidence of activity is found chiefly at or below the surface of the soil. A somewhat longer illumination period, on the other hand, favors reproductive activities followed by leaf fall and dormancy or death. In such plants, therefore, abrupt change from a long to a very short day will not lead to shedding of leaves but will result in diverting developmental activities downward in the plant, the leaves remaining intact and doubtless functioning in some measure. The above-mentioned two sumacs and tulip and other woody species were exposed to a 10-hour day during the summer months. Under these conditions none of the plants shed their leaves but, instead, assumed a generally unthrifty appearance and ceased upward growth. The leaves became dark green in color and to the touch appeared to contain but little sap. These results indicate that a gradual

transition from the long days of summer to the short days of midwinter is required to induce abscission in these plants.

DORMANCY AND DEATH

In general, exposure of annuals to the optimal illumination period for flowering tends to induce rapid senescence and death. In the same way exposure to certain definite day lengths causes perennials to enter into a state of dormancy. Deciduous trees and shrubs, in which the laying down of resting buds on the stem precedes leaf fall, enter into a form of dormancy involving temporary weakening, but not complete loss, of capacity for apogeotropic functioning. Herbaceous perennials enter into a form of dormancy in which there is more complete loss of the apogeotropic function. In both cases there is loss of leaves and photosynthetic activity is mostly suspended. That the first-named type of dormancy may be prevented by maintenance of a relatively long illumination period is shown by the experiments with the tulip poplar described in the preceding discussion of abscission and leaf fall. That the second type of dormancy also may be prevented by maintaining a long illumination period has been shown in experiments with *Aster linariifolius*.

Too great a departure from the optimal illumination period for apogeotropic growth, however, may cause the plant to assume a sort of pseudo-dormancy in which the leaves acquire an abnormally dark green color and the general appearance above the ground is one of comparative inactivity. Annuals, as well as perennials, show this response. These considerations lead to the conclusion that there may be an optimal light duration for death as well as for dormancy, while on either side of this optimum there may be very considerable and long-continued activity by the plant. On the one side the response is primarily and characteristically apogeotropic. On the other side the general tendency is toward geotropic response, visible expression being confined mostly to the surface or underground portions of the plant.

The results of tests with five varieties of soybeans will illustrate the fact that exposure to a definite light period results in rapid senescence and death in annuals. The varieties known as Mandarin, Peking, Tokyo, Biloxi, and Otootan were planted May 31 to June 1 in boxes and germinated June 4 to 6. They were exposed to day lengths of 10, 11, 12, 13 hours, and to the natural length of day of summer. For comparison, a lot of each variety also was given 10 hours of light daily of low intensity by means of a shade of cheesecloth. The principal results of the tests are presented in Table VI. On September 8 the seed pods of all varieties were fully matured and dry under all reduced day lengths, but only those of the Mandarin variety had matured under the natural length of day. Under the shorter light period all varieties flower at practically the same time; but as the light duration is increased the dates of flowering draw apart, and under the full summer day length the differences in time of flowering become very great. As to the advance of senescence following the flowering and fruiting stages two facts are brought out in the table. It is evident that the rate at which senescence advances in a given variety depends on the duration of the light period and, also, it is evident that the optimal light period for advance of senescence differs with the variety. For the earlier varieties, Mandarin and Peking, it appears that the optimal period is approximately 13 hours, while for the very late varieties, Biloxi and Otootan,

the optimal is 11 to 12 hours. The Tokyo seems to be better able to resist the advance of senescence than the other varieties. The Peking is particularly responsive to a definite light exposure in this respect and under the 13-hour day began shedding its leaves early in August.

TABLE VIII.—*Behavior of different varieties of soybeans planted May 31 to June 1 and grown under daily light exposures of different lengths.*

Treatment.	Average height of plants on Aug. 5.					Time of first blossoming.				
	Mandarin.	Peking.	Tokyo.	Biloxi.	Ototan.	Mandarin.	Peking.	Tokyo.	Biloxi.	Ototan.
10-hour day, 5.30 a. m. to 3.30 p. m.	*In.* 18	*In.* 13	*In.* 15	*In.* 18	*In.* 23	June 27	June 25	June 27	June 30	July 1
11-hour day, 5.30 a. m. to 4.30 p. m.	20	14	20	20	25	...do....	...do....	...do....	...do....	Do.
12-hour day, 5.30 a. m. to 5.30 p. m.	20	16½	20	21	30	...do....	...do....	...do....	July 2	July 4
13-hour day, 5.30 a. m. to 6.30 p. m.	27	19	27	28	36	...do....	...do....	June 30	July 5	July 6
Controls, full summer day length	25	17	51	31	33	July 2	July 18	Aug. 8	Sept. 7	.....
10-hour day, 5.30 a. m. to 3.30 p. m., under heavy shade	18	11	15	18	33	June 28	June 27	June 28	June 30	July 2

Treatment.	Appearance of plants Sept. 8.				
	Mandarin.	Peking.	Tokyo.	Biloxi.	Ototan.
10-hour day, 5.30 a. m. to 3.30 p. m.	Leaves green	Leaves green	Leaves green	Leaves yellowing.	Leaves yellowing.
11-hour day, 5.30 a. m. to 4.30 p. m.	Leaves yellowing.	Most leaves green.	.....do.....	Mostly leafless.	Leafless.
12-hour day, 5.30 a. m. to 5.30 p. m.	Few green leaves.	...do.....	.....do.....	Few green leaves.	Few green leaves.
13-hour day, 5.30 a. m. to 6.30 p. m.	Leafless.....	Stalks dead, leafless.	.....do.....	Most leaves green.	Leaves green.
Controls, full summer day length.	Nearly leafless.	Leaves green	Green, still flowering.	Still growing.	Still growing.
10-hour day, 5.30 a. m. to 3.30 p. m., under heavy shade.	Mostly leafless.	...do.....	Leaves green	Few green leaves.	Leafless.

Considering that a light period which is unfavorable for vegetative activity may cause death or dormancy, as the case may be, the question arises as to the relation of the light period to emergence from dormancy. The line of division between death and dormancy is often a very narrow one, and there are varying degrees or conditions of dormancy. It appears that the time and conditions of emergence, or whether it shall occur at all, may depend in part upon the length of day under which the plant enters upon the state of dormancy. The behavior of the Kudzu vine (*Pueraria hirsutus* (Thunb.) Scheid.) in this particular is of interest. Beginning May 12, seedlings which had been growing since January 5 were given a 10-hour day through the summer while control plants were exposed to the full day length. Under the 10-hour day growth of the aerial portions of the plant soon ceased and the foliage assumed a very dark green color. The basal portion of the stem became considerably enlarged. The controls grew vigorously through the summer. Both lots of plants were transferred to the greenhouse September 15. In both cases the leaves gradually withered and fell and the plants became dormant, although this condition was not fully reached till early in December. By January 11 new shoots

began to appear on the plants which had been exposed to a 10-hour day during the preceding summer. The renewed growth was rapid and vigorous. The new foliage showed the abnormally dark green color of the original leaves which had developed under the 10-hour day. The control plants did not renew their growth till February 16 (Pl. 15, A and B). Beginning August 16, a third series of plants were placed in the greenhouse artificially lighted from sunset till midnight. In this case dormancy was inhibited and rapid growth continued during the winter months. Moreover, no woody stems were formed, even the tissues of the basal portions of the stem remaining soft, in contrast with the usual behavior of Kudzu.

As has been repeatedly pointed out, there is a well-defined quantitative aspect of the influence which the length of day exercises on the formation of seeds and vegetative resting and reproductive structures so that, other conditions equal, it is to be expected that emergence from the rest period will be materially influenced by the prevailing length of day under which the state of dormancy was developed. There can be no doubt that both the quantity and the character of the plastic "reserve" material available for subsequent needs of the resting embryo are conditioned in large measure by this factor.

As regards the direct action of length of day on emergence from the rest period, it would seem that successful emergence without the aid of a favorable day length will depend on whether suitable temperature conditions and other environmental conditions can set in action the necessary internal processes for renewing active growth. Since ultimately both the character and the extent of growth in the plant are dependent largely on the prevailing day length, the point at which this factor must intervene in the renewal of activity by the resting structure will be governed by the amount of potential growth energy that becomes available from stored materials under the existing environment. In the case of the vegetative bud the action of a favorable light period may come into play almost at the outset. What action, if any, the light period may exercise directly on nonchlorophyllous structures can not be stated at this time. It has been shown by MacDougall (*13*) that in certain cases resting buds attached to large storage organs may maintain renewed growth for a year or more without receiving any light. By way of contrast, however, the behavior of *Hibiscus moscheutos* L. is of interest. Under short day conditions this plant is unable to make appreciable growth (*7, p. 578*). Seedlings were grown in buckets during the summer under outdoor conditions and were left out of doors during the following winter. Beginning March 27, one series was allowed to receive only 10 hours of light daily while a second series continued to receive the full seasonal period of daylight. On these control plants new shoots apeared April 8 and 9 and growth continued in normal fashion. Under the 10-hour day a feeble development of new shoots was noticeable by May 18, but these soon died when still less than an inch long. The condition of the plants under the two conditions of light on June 21 are shown in Plate 17, B. Similarly, *Aster linariifolius* was transferred to the greenhouse October 17 and on November 27 was placed beneath a 100-watt electric light provided with reflector, at a distance of 1 foot, the light being on each day from 4.30 p. m. to 12.30 a. m. New shoots appeared during the third week in December. Under control conditions the rest period was not broken till spring. In the case of second-year beets, previously described (p. 888), although development of flowering stems began under a 10-hour day, the plants were never able to flower. A number of small trees and

shrubs, including *Acer negundo* L., *Acer rubrum* L., *Cornus florida* L., and *Rhus glabra* L., which were exposed to an 8-hour day, beginning early in January, successfully unfolded their leaves at about the same time as did the controls. Some of these, however, made but little subsequent growth even under a 10-hour day, which proved to be too short for their requirements. It appears, therefore, that there are all degrees of dependence upon the direct action of the light period in the matter of emerging from dormancy. Much, doubtless, depends on the conditions under which the plant enters dormancy and the environmental conditions which prevail during the rest period. The whole subject of dormancy in relation to the light period will require further study before general conclusions may be drawn.

SENESCENCE AND REJUVENESCENCE

All experimental data thus far secured seem to support the conception advanced long ago that a common cause of general senescence, that is, senescence of the whole or greater part of the plant, is the intense formation of independent or semi-independent reproductive structures. In annuals a length of day which favors intense flowering and fruiting has resulted in rapid senescence and death, and in herbaceous perennials this has been true with respect to both sexual reproduction and tuber formation. This relationship applies whether the optimal light period for reproduction corresponds to the longest summer days or the shorter days of spring and fall. It has been pointed out that Peking soybeans rapidly pass into senescence under the influence of a day length of about 13 hours, which approximates the optimal length of day for flowering and fruiting. Under a light period much in excess of, or much below, 13 hours senescence is deferred. *Convolvulus tricolor* L. furnishes an example of how a light period too short to admit of flowering may indefinitely delay decline and death. Seedlings exposed to a 10-hour day, beginning June 8, were unable to blossom, while growth continued for a period of more than eight months. In this instance the plant attains an abnormally large size by continued exposure to a light period too short to admit of flowering.

Localized senescence is a very common feature of photoperiodism and, of course, is frequently accompanied by regeneration phenomena. When Cosmos, for example, is exposed to a long day, continued elongation of the axis is accompanied by progressive loss of lower leaves. As the light period becomes less favorable for apogeotropic response the tendency is in the reverse direction. In various species there may be simple abscission and leaf fall, accompanied by formation of resting buds; branching, as a result of loss of dominance on the part of the apical bud, followed by decline of the latter; progressive decline of the upper portions of the primary axis; a general transfer of activity from above to the ground level or even to subterranean parts. Examples of all these stages have been presented in the preceding pages.

Since certain light periods may defer the appearance of senescence, the question arises as to whether exposure to these light periods may effect rejuvenation in cases of advanced decline and impending death. Examples of this type of rejuvenescence were given in the previous paper (7, *p.* 567) in the cases of soybeans, *Ambrosia artemisiifolia* L., and wild aster. *Bidens frondosa* L. also furnishes an excellent example.

As reported in the former paper, this species flowers precociously under the short days of winter but flowering is readily inhibited by lengthening the light period. The two phases of activity are represented in a single plant in Plate 16, A. Under the natural day length of winter this plant flowered early in February at a height of 5 inches. At the time of flowering the plant was transferred to the greenhouse electrically lighted from sunset till midnight. The original stem died to the ground, but under the lengthened light period new shoots appeared and these reached a height of more than 4 feet. It seems clear that in typical annuals not only may general senescence be deferred more or less indefinitely by preventing exposure to the particular light period which favors reproductive activities but even after this stage has been reached rejuvenescence may be effected through regenerative processes. The final stages in an interesting type of rejuvenescence in the inflorescence of poinsettia, the earlier stages of which are referred to on page 903, are illustrated in Plate 19, B.

LOCALIZATION OF THE PHOTOPERIODIC RESPONSE

An experiment was made with Cosmos to determine whether the stimulus imparted to a particular portion of the plant by change in the light period extends its influence to other parts of the individual. The results were clean cut, and some interesting facts were brought out. Young seedlings, propagated under long-day conditions, were cut back to the first node above the cotyledons so as to cause two opposite branches to develop. A month after the plants were cut back a cardboard screen was interposed vertically between the branches of each individual, the plane of the screen extending in north-and-south direction. On one side of the screen a 100-watt electric light, with reflector, was turned on each day from sunset till midnight. On the other side of the screen only the natural daylight period of the winter season prevailed. The plants were so adjusted with reference to the screen that the portion of the plant below the point of origin of the two branches was on the long-day side in some instances and on the short-day side in others. In all cases the branches exposed to the short day promptly flowered while those exposed to the long day continued the sterile, vegetative type of development, without regard to the exposure of the basal portions of the plant. Moreover, in all cases the sterile branch assumed a dominant influence over the basal portion; that is, the basal portion of the plant continued to enlarge in harmony with the growth of the vegetative branch while the flowering branch soon ceased growth and passed into a state of decline. These relations are clearly shown in Plate 16, B. In this connection it is to be recalled that the determinative influence of the light period on an aerial part may be transmitted to a subterranean part of the plant, as shown in the case of the potato. In this instance the apogeotropic influence of the long light period inhibited tuber formation and, instead, buds at the nodes of the stolons were caused to germinate without a rest period, thus forming offsets. The experiment with Cosmos shows that such influence on an aerial plant part may not be transmitted to another coordinate member, and to this extent perhaps the stimulus may be regarded as localized. It is not entirely clear as to how or why the branch exposed to the longer light period is dominant over the branch exposed to the shorter light period in its influence on other portions of the plant.

LIGHT PERIOD IN RELATION TO OTHER FACTORS OF THE ENVIRONMENT

To arrive at a satisfactory conclusion as to the practical significance of the seasonal range in length of day in plant growth it is essential, of course, to know to what extent other environmental factors are likely to modify the action of the length of day. Because of the unvarying regularity of the annual cycle in day length it is apparent that any influence of this factor on plant behavior will find expression in the normal or usual seasonal periodicity rather than in unusual or occasional responses. In short, the change in length of day may be expected to bring about the usual rather than the unusual in the annual cycle of the plant's activities. On the other hand, occasional severe drought, abnormally high or low temperatures, unusual chemical conditions of the soil, attacks by insects or diseases, may cause temporary disturbance either qualitatively or quantitatively in the usual seasonal development of the plant.

The question of chief interest in the present connection is the extent to which the normal sequence of seasonal changes in other climatic factors may modify or nullify the influence of length of day on periodicity in plant activity. That various climatic factors, as well as the factor spoken of as soil fertility, may produce quantitative differences is known to all. To what extent the actual annual range in these factors may cause distinct qualitative differences in expression is not so well understood. In connection with the present investigations a limited number of observations have been secured with certain species on the significance of climatic factors other than change in the light period in phenomena of plant periodicity.

As is well known, the seasonal change in the lengeh of day is accompanied by important changes in the intensity of the sunlight and in its quality, that is, in the energy distribution of the visible portion of the sun's spectrum. Hence, it is of special interest to consider these factors in relation to photoperiodism. In the earlier paper considerable data were presented (7, *p. 581 et seq.*) tending to show that reduction of the intensity of the sunlight in summer to as low as one-third the normal had no appreciable effect on the time of flowering of soy beans. These results have been confirmed in the experiments referred to on page 905. As a part of the tests a long, rectangular frame, with sides and top covered with cheesecloth, was erected over a portion of a steel track leading into the dark house so that a truck carrying one lot of the plants could be rolled under the shade each day while a second lot was exposed to the direct sunlight. A series of measurements of relative light intensity within and outside the shade from 10 a. m. to 3 p. m. on July 27 were made by R. A. Steinberg, of this office. For the purpose a Sharp-Millar model F photometer, tested by the United States Bureau of Standards and found to be accurate to between 5 and 10 per cent, was used. In round numbers the average intensity thus obtained for the period indicated was 10,500 foot-candles in the open and 3,500 foot-candles under the shade. The results of this test of the comparative effectiveness of light duration and light intensity are given in Table VIII. The maximum effect of a reduction in light intensity to one-third the normal, with a light period of 10 hours, was to delay the date of first flowering by one to two days. In marked contrast, a reduction in the length of the daily light period from the average natural summer day length of about 14½ hours to 13 hours, a decrease of about 10 per cent, promptly initiated

flowering in every case. The vegetative period of the Biloxi variety, for example, was reduced from 94 days to 21 days. In this experiment the reduction in the duration of the daily light period was no greater than actually occurs during the growing period of the Biloxi. The light intensity was reduced by shading to about 3,500 foot-candles, while the natural decrease up to the close of the growing season (October 1) only is to an average of about 6,200 foot-candles for the same hours of the day (9 a. m. to 3 p. m.), and to about 4,500 foot-candles for the entire 10-hour day (7 a. m. to 5 p. m.). It is to be noted, also, that the reduced intensity shows no selective action on the different varieties with respect to time of flowering, whereas this is the characteristic feature of the varietal response to change in light duration. The varietal responses to the different light periods, in fact, are strictly in accord with the natural behavior of the varieties as to earliness of maturity. There are significant differences, also, in the effects of change in intensity and change in duration of the light on the heights attained by soybeans. In the former paper (7) it was shown that under the natural day length of summer, reduction of light intensity causes increased elongation of the stem in soybeans and that, in fact, with heavy shading a typical viny form of growth develops. In Table VI it is shown, however, that under a 10-hour day heavy shading failed to cause increased stem elongation in comparison with plants exposed to the full sunlight for 10 hours daily, except in the case of the Otootan variety. The effect of shortening the duration of the light period is the reverse of that produced by reducing the intensity; that is, there is decided reduction in stem growth, as is shown in Table VI. Here, again, the effect of a shortened light period on the stature attained by the plant is in accord with the progressive decrease in stature which results when the date of planting is made later and later in the season, an effect well shown in the former paper (7, *Pl. 78, B*). Decrease in light intensity fails to account for either the initiation of flowering or the slowing down in stem growth in soybeans which occur with advance of the season after the summer solstice.

A similar experiment was made with the Silverskin onion, using the same shade that was employed in the test with soybeans. With the light intensity thus reduced to one-third the normal, plantings of the onion made June 16 grew and developed bulbs in substantially the same manner as in the open sunlight. At most, the dying back of the tops was delayed a week and the bulbs were about the same size as those of the controls. Under a 10-hour exposure to full sunlight, on the other hand, there was no bulbing and the tops remained green throughout the summer. These differences in behavior are well shown in Plate 18, A. There is no evidence, therefore, that bulb formation in the onion is due to excessive intensity of sunlight in the summer.

In the light of these experiments it would seem that use of such terms as "quantity of solar radiation" in relation to specific plant responses should be abandoned where such terms involve both intensity of the radiation and duration of the daily exposure. Not only is there frequently no approach toward equal effects for equal changes in these two factors but these effects may actually be in opposite directions. The futility of attempting to apply quantitative energy relations of this sort to the process of flowering in the soybean plant is further emphasized in the following data. Beginning June 30, one lot of Peking seedlings was placed in darkness from 10 a. m. to 4 p. m. daily; a second lot was simi-

larly darkened from 10 a. m. to 2 p. m.; while a third lot was excluded from the light only during the early morning period prior to 6.30 a. m. Controls were exposed to the full day length, averaging 14 hours and 33 minutes (sunrise to sunset) for the month of July. The dates of first flowering in the four series were August 5, August 5, July 27, August 10, respectively. It is estimated that in the first three series the reduction in sunlight by darkening amounted to approximately 65, 48, and 2½ per cent, respectively, of the total for the day. It is evident that a reduction of 2½ per cent in the amount of sunlight when applied in the morning was more effective in initiating flowering than a reduction of 65 per cent applied in the middle of the day. With respect to flowering, the remarkable sensitiveness of soybeans to change in length of the daily light period is emphasized in the behavior of successive field plantings of the Peking; those germinating, for example, on July 20 showed a vegetative period 8 to 10 days shorter than those germinating July 5, while the change in length of day in the interval of 15 days was only about 17 minutes, or 2 per cent. It should be noted in this connection that Rivera (*20*), as a result of his investigation, considers that the duration of the daily illumination period is more potent than the intensity of the light in influencing crop yields.

To obtain direct experimental evidence on the possible significance of the seasonal change in the quality or the composition of sunlight in the development of the plant offers considerable difficulty, although this phase of the subject is now under investigation. The indirect evidence available at this time seems to indicate that this factor is not of great importance, at least for the species under study. For example, flowering is easily induced in midsummer by shortening the day length through cutting off the morning and late afternoon sunlight. The plant in this case receives a maximum proportion of sunlight of the shorter wave lengths. Flowering also occurs, however, through natural shortening of the day length in fall and winter, and in this case the plant receives a greatly reduced proportion of the shorter wave lengths.

As is more fully brought out in the final chapter of this paper, it seems likely that the internal water supply of the plant is of fundamental importance in photoperiodism. Nevertheless there is no definite seasonal change in rainfall in the eastern United States which would account for seasonal periodicity in plant activities. It is necessary to distinguish between the internal mechanism of the plant concerned in regulating the water content, on the one hand, and the external water supply, on the other. In the previous paper (7) detailed data were given to show that wide differences in the water content of the soil were without appreciable effect in initiating flowering in soybeans. By reference to the experiments with *Sagittaria latifolia* recorded on page 878 it will be seen that growing this plant as an aquatic under a 10-hour day delayed flowering by only about two weeks as compared with cultures under mesophytic conditions. The reduction in the light period, on the other hand, shortened the vegetative period by more than two months.

Temperature undoubtedly is the most important environmental factor in relation to the action of the light period on plant growth, and two phases of its action need to be taken into account. In the first place, the general tendency toward an increased rate of growth and development as the temperature increases, within favorable limits, and the reverse tendency with decrease of temperature should be to delay or even inhibit flowering of typical summer annuals in late summer or fall.

For this reason decrease of temperature with advance of the season could not be expected to account for the initiation of flowering in soybeans in August and September, the tendency being in the opposite direction. Direct evidence on this point is furnished by plantings of the Peking and Biloxi varieties made in the greenhouse on December 14 under controlled conditions of temperature, with and without electric illumination from sunset till midnight. With a mean temperature of approximately 72° F. and a daily temperature seldom exceeding in either direction a range from 65° to 75°, the soybeans germinated December 19 and, with natural illumination only, the Peking began flowering January 25 and the Biloxi February 25. With the added artificial illumination, flowering was inhibited. With a mean temperature of approximately 55° and a daily temperature seldom exceeding in either direction a daily range from 50° to 60°, the soybeans which germinated December 27 had not flowered March 1 under either light exposure. In the first case the mean temperature (close to 72°) was somewhat below the mean temperature for the month of July at Washington (76°.8). In the second case the mean temperature (approximately 55°) was considerably below the Washington mean of 68° for the month of September. It is clear that the lower temperature delayed the time of flowering.

A second phase of the temperature effect seems to relate more directly to internal conditions of nutrition, especially affecting, perhaps, the balance between income and outgo of carbohydrate because of the change in the rate of respiratory activity. In this way the relation between the duration of the light period and the prevailing temperature may become of decisive importance. The requirements for successful flowering necessarily are more critical than for vegetative growth, since the floral structures are dependent on other parts of the plant for their supply of suitable forms of carbohydrate. Unfavorable conditions of balance, therefore, either because of reduced income or excessive outgo of carbohydrate, may easily inhibit flowering and fruiting. These conditions would not necessarily check development of the green parts of the plant, since such structures tend to be self-supporting with respect to carbohydrate supply. It need only be added that in these considerations the form of the carbohydrate as well as the quantity must be taken into account.

It has been demonstrated that for many species, probably the majority of them, the extremely short days of winter in higher latitudes will inhibit increase in stature, and in many cases flowering and fruiting also. Largely as a result of the transition from the longer summer days to the shorter days of winter many annuals are caused to die and many perennials are forced into a state of more or less complete dormancy. Hence, the income from photosynthesis is reduced to a minimum. It is obvious, therefore, that exposure to a relatively high temperature during the short days of winter may easily prove disastrous to the plant. The importance of exposure to cold during the winter rest period has been recently emphasized by Coville (*6*). Exposure to the forcing action of high temperatures in winter is likely to be especially unfavorable to reproductive structures. It is well known, also, that in some way exposure to cold may exercise a beneficial action on nonchlorophyllous resting organs, resulting eventually in renewed activity. In general, when the dormant structure has entered upon the rest period with the necessary "reserve" materials the initial processes of renewed activity may be stimulated by favorable temperature conditions, such as a period

of chilling. The extent to which these renewed activities may progress after they have been initiated in the absence of a favorable light period, however, is extremely variable, as was pointed out on page 907. There seems to be no question as to the importance of the relationship between the action of the seasonal decrease in length of day in forcing the plant into a state of relative inactivity, on the one hand, and the effect of the cold of winter in promoting successful emergence from the rest period by conserving and bringing into play the stored energy of the resting organ, on the other hand.

RANGE OF RESPONSE TO LENGTH OF DAY

It is apparent that species differ widely in their sensibility to change in the length of day and in the form of expression which the response may take. Cosmos continues elongation of the vegetative stem under any day length in excess of about 13 hours, while under all day lengths much below 13 hours flowering readily takes place. Mikania may maintain sterile vegetative growth under the extreme day length (in excess of 15 hours) of summer in high latitudes. It flowers readily under a daily light period of about 14 hours, while both growth and flowering are inhibited by a light period of 13 hours or less. Goldenrod forms a flowering stem under any length of day in excess of approximately 8 hours, but with a shorter light period only the leaf-rosette type of development is possible. Sorrel (Rumex) forms aerial flowering stems when exposed to the long days of summer, but under the short days of winter only the underground type of stem is formed. Artichoke is unable to flower under a light exposure of 10 hours or less, but under these conditions there may be intense tuber formation. Under a 10-hour day groundnut (Apios) is unable to flower, there is no elongation of aerial stems, the number of new underground tubers is greatly reduced, and the mother tuber is materially enlarged. Under a longer day length all of these forms of response in groundnut are reversed. The Mandarin soybean flowers under the longest summer days at Washington, while the Peking does not begin flowering till the latter half of July, the Tokyo about two weeks later, the Biloxi some three weeks later still, and, finally, the Otootan about September 15—all in response to the prevailing day length. In the violet the extreme seasonal range in day length from early spring to midsummer suffices only to change the type of blossom from the blue petaliferous to the cleistogamous form. Finally, in buckwheat flowering occurs throughout the range of day length from 5 to 18 hours, although under the shorter period it behaves as an ephemeral, and under the longer period it assumes the form of a giant everbloomer.

It may be considered that there is a wide range or "scale" of response to change in the light period and that the portion of this scale covered by the individual species or variety is extremely variable. For example, buckwheat through all ranges in length of day prevailing in the temperate zone occupies only that portion of the scale lying between the strictly flowering condition and the sterile, giant type of development. The bean referred to on page 893 occupies the portion of the scale represented in the strictly sterile giant form, the flowering condition, and the phenomenon of tuberization. No single species has been observed which manifests all forms of response, but one might perhaps conceive of a sort of composite plant, combining the responses of several different species and thus covering the entire range. Beginning with one of the extremes of this

range of response, there would be an optimal light period for elongation of the vegetative stem or increase in stature. Under this optimal light period, which in the first instance will be assumed to correspond with the longest days of summer, there would be more or less indefinite elongation of the primary axis, with no branching and a minimum of foliage development (Cosmos). Any departure from the optimal light period would check stem elongation; and, as a result, a chain of responses would come into expression as the light period became progressively less favorable for increase in stature. The first effect of outstanding importance would be flowering and fruiting; and, as a result of partial loss of dominance in the apical bud, branching might occur at this stage (Cosmos). The change in the light period may be such as to direct the plant's energies more or less quantitatively toward flowering and fruiting, in which case senescence and death would be the logical outcome, the plant behaving as an annual. Even in this case, however, rejuvenescence may be effected under favorable conditions by a return of the optimal light period for vegetative growth, the plant thus escaping death (Bidens). Between the respective optimal light periods for stem growth and for sexual reproduction there would be a buffer zone in which combined growth and flowering would occur, thus representing the everblooming condition (Viola).

With a further departure from the optimal light period there would be more or less complete inhibition of stem elongation, resulting in intense tuberization; that is, stem elongation would be replaced by stem thickening. In this case flowering would be inhibited (artichoke). If a primary axis had previously developed, there would be a general downward transfer of activity to the ground level or even beneath the soil surface. The end result would be the formation of underground resting structures, as rhizomes or tubers. Here, again, between the respective optimal light periods for flowering and for tuberization there would be an intermediate zone in which important responses find expression. There may be combined flowering and tuberization (groundnut). Aerial and underground types of tuberization are alternative forms of expression (cinnamon vine). Aerial branching may give way to underground branching (sorrel). The stemless leaf rosette, with or without tuberization, is an important type of activity falling within this zone. Here would be placed the flowering herbaceous perennial which flowers and fruits so freely as to cause the death of the aerial parts but with sufficient regenerative energy remaining to organize underground perennating structures. The final response would be death as a direct result of starvation when the light period has become too short to furnish sufficient photosynthetic material to support any form of activity. The circumstances of death in this case are quite different, however, from those which induce intensive fruiting and thereby result in the death of the mother plant. It is to be understood, of course, that all forms of expression are conditioned on the existence of general environmental conditions falling within the limits of tolerance of the species in question.

The above-mentioned series of responses would result from a progressive decrease in the duration of the light period. Assuming an optimal light period for stem elongation corresponding to the intermediate day length of spring and fall, a somewhat different chain of events, not yet fully determined, seems to result from exposure to light periods of excessive length. Probably one of the first notable effects of a light period in

excess of the optimal for stem growth is the laying down of flower buds. It is possible, also, that resting vegetative buds of woody perennials result from these conditions, although this has not been definitely determined. It has been shown that bulb formation commonly results as one of the final effects of an illumination period of excessive duration. No example of death from this cause has yet been encountered.

These outlines of the series of responses initiated by graded departures from the optimal light period for stem growth are necessarily tentative. All responses are not included, and it is possible that the proper sequence of those which have been given will ultimately require modification in some instances.

NATURE OF THE REGULATORY ACTION OF LENGTH OF DAY

Definite conclusion as to details of the internal processes concerned in the phenomena of photoperiodism is withheld, pending the completion of fairly extensive biochemical investigations now in progress in this office. For the present only the more general aspects of the problem as brought to light in the response of the plants as a whole will be considered. These various forms of response seem to indicate clearly that in some way the internal water supply, the degree of hydration, of the living cell content is subject to very delicate regulation by change in the ratio of the number of hours of light to the number of hours of darkness in the daily period of 24 hours. It will be observed that there is an optimal light-darkness ratio for maximum rate of stem growth, and Chandler (*5*) and Reed (*19*) have shown that maximum growth is correlated with a dilute cell sap or high degree of turgidity. In recent years MacDougall (*14*) has especially emphasized the significance of hydration in growth phenomena. The various responses of the plant coming into expression as the light period becomes progressively less favorable for upward stem growth are practically without exception those more or less associated with relatively xerophytic conditions. Tendency toward increased flowering and fruiting, increased branching, pubescence, abscission, and leaf fall, the general tendency toward stem shortening, tuberization, and increased underground stem development are phenomena in point.

The behavior of *Viola papilionacea* under different light periods furnishes direct evidence on this subject. During the shortest days of winter the plants are in a semidormant condition, the young leaf buds becoming tuberized through loss of power to elongate the leaf petiole. Under the intermediate day length of spring leaves with short petioles and blue blossoms with relatively short stems make their appearance. During the long days of summer the petioles of the leaves are greatly lengthened. When plants bearing the summer type of leaf are abruptly transferred to short-day conditions partial collapse occurs within two or three days, obviously due to loss of turgidity in the leaf stem. In due course, also, the characteristic spring type of blue blossoms reappears. This behavior is shown in Plate 18, B.

Without at this time raising the question as to the exact mechanism of the internal processes affected, it seems possible that highly refined regulation of the degree of hydration of the protoplasm furnishes a basis for the various responses of the plant to changes in the light period. It is believed, however, that this regulation is effected primarily through direct action on the internal mechanism which maintains hydration rather than by merely influencing external factors which modify relative

gain and loss of water. This implies, perhaps, control of permeability. Proper distinction must be made, therefore, between regulation of the external supply of water and control of the internal mechanism involved in dealing with phenomena of hydration. It seems probable that the light period, acting through control of the internal mechanism, is capable of exercising a far more refined regulation of the internal water supply of the plant's parts than is ordinarily accomplished by change in the external supply of water. The experiments with Sagittaria recorded on page 878 indicate that this is true. Growing this plant as an aquatic at most delays flowering by some 10 days as against growth under mesophytic conditions, while appropriate change in the light period resulted in sharp response. As already pointed out, growing soybeans under semixerophytic conditions in contrast with mesophytic conditions was entirely without effect in initiating flowering. It may occasionally happen, perhaps, that the available external supply of water will be just right to favor a definite response such as successful flowering. It seems likely also that plants which are not particularly sensitive to change in the light period, including typical everbloomers, such as the cotton plant (*Gossypium* spp.), may be more subject to disturbance of the normal flowering and fruiting processes (shedding of blossoms or young fruits, etc.) by such factors as change in the water supply or the ratios between the different elements of plant food in the soil. In addition to its apparent regulatory action on the internal mechanism controlling hydration, it is to be expected that the duration of the light period will tend to modify the external evaporative forces involved in transpiration. It seems possible that this may be a factor of importance in the action of the long days of summer in checking the growth of certain plants, although no definite evidence on the subject is available.

Regardless of its actual causative significance, there seems to be no doubt that hydration is subject to definite regulation by length of day and, hence, change in the degree of hydration is definitely correlated with change in form of expression in the plant. Apparently the optimal light period for apogeotropic growth also is optimal for maximum hydration. Progressive loss of power to fully utilize carbohydrate and other nutrient material in accomplishing increase in stature seems to be correlated with progressive loss of capacity to maintain the transpiration stream. Development of sexually produced as well as vegetative reproductive structures, tuberization, and the general phenomena of dormancy seem to follow as natural sequels.

CONCLUSION

In this paper considerable data are presented which tend to demonstrate the importance of the seasonal range in length of day as a factor in initiating and regulating sexual reproduction in plants, thus confirming the results of investigations reported in an earlier article. Experiments are described, also, which bear on certain quantitative aspects of this response. Results of fairly extensive investigations on the relation of length of day to the formation of tubers and bulbs are presented in some detail. Observations, largely of a preliminary nature, are reported on length of day as a factor in various other responses of the plant, including character and extent of branching, root growth, formation of pigment, abscission and leaf fall, dormancy, and rejuvenescence. Apogeotropic growth or increase in stature as affected by the daily light

period is given somewhat detailed consideration in its apparent relation to flowering and fruiting and the other responses mentioned.

It appears that the duration of the daily illumination period not only influences the quantity of photosynthetic material formed but also may determine the use which the plant can make of this material. The evidence available at this time indicates that for each species there is an optimal light period for maximum upward elongation of the stem or increase in height. For some species this optimal light period is furnished by the longest days of summer in the temperate zone while for other species the intermediate length of day of spring and fall is optimal. In the latter group of plants the excessive length of day of midsummer probably initiates flowering, and in the case of some woody perennials the formation of resting vegetative buds. Certain species, moreover, are caused to die back, form bulbs, and enter into a midsummer rest period.

In the first-named group of species progressive shortening of the daily light period initiates a series of responses, including flowering and fruiting, tuberization, character and extent of branching, dormancy, all of which are prominent features in annual periodicity. Reducing the light period below the optimal for stem elongation by a certain definite decrement tends to divert the plant's activities more or less quantitatively toward sexual reproduction. There seems to be an optimal light period, therefore, for flowering and fruiting. Exposure to this optimal light period commonly induces rapid senescence and death, as typified in annuals, probably as a result of the intense flowering and fruiting. With day lengths ranging between the optimal for growth and the optimal for sexual reproduction the tendency toward division of the plant's energies between these two types of activity is manifested in the everblooming or everbearing condition, shifting of the quantitative relationship between relative vegetative and reproductive activity, change in the size of the individual fruit or seed, delayed and sparse flowering and fruiting, cleistogamy, and other abnormalities. Moreover, in the natural seasonal change in length of day there is considerable difference between the effects of the change away from the vegetative optimum toward the flowering and fruiting optimum and those resulting from the change in the opposite direction. Data of interest have been presented, also, on the time required for imparting the stimulus or condition for flowering by appropriate change in the light period.

Further reduction of the light period by a sufficient decrement below the optimal for sexual reproduction tends to induce intense tuberization, a feature marking the final stages in reduction of stem elongation. There is a more or less clearly defined optimum for tuberization. Here, again, with a light period ranging between the optimal for tuberization and the optimal for flowering there is a tendency toward division of the energies of the plant between these two features of development. Under these conditions sexual reproduction and tuberization may proceed simultaneously, a division of activity which is commonly seen in herbaceous perennials. Tuberization as a result of decrease in the daily light period involving deposition of carbohydrate in relatively condensed or dehydrated forms indicates marked loss of power to utilize the product of photosynthesis in elongating the stem or in developing flower and fruit. It is most typically associated with the stemless or rosette form of foliage development, representing, perhaps, maximum divergence between income and effective utilization of the photosynthetic product for promotion of growth.

One of the characteristic effects of change in the light period from optimum to suboptimum for stem elongation is to promote branching. Thus, the apical bud loses its dominance and lateral buds become active. As stages in the response to progressive departure of the light period away from the optimum for elongation of the axis may be noted increased branching at the top, middle, or base of the aerial portion of the axis; various degrees in erectness of the resulting branches; change from aerial to underground type of stem and change downward in direction of growth of these underground stems.

The decreasing length of day of fall is an important factor in causing perennials to enter upon the winter period of dormancy. Abscission and leaf fall, also, appear to be induced by this shortening of the light period. Abrupt and sufficiently pronounced change from long-day to short-day conditions, however, tends to cause deciduous woody perennials to behave like evergreens in retaining the foliage leaves, and this tendency also is discernible even in certain typical annuals. Furthermore, the light period, through quantitative features of its action on the formation of vegetative resting and reproductive structures, may affect to some extent the conditions of emergence from dormancy.

During the winter months the relation between the length of the daily light period and the temperature becomes especially important. Because of the short days prevailing in this period the income of the plant through photosynthesis is reduced to the minimum and growth conditions are otherwise unfavorable, so that high temperatures are likely to establish an unfavorable ratio of income to outgo and thus may easily prove disastrous to the plant.

It seems probable that the annual cycle of length of day, affording as it does the only consistently rhythmic feature of the external environment, is a dominant causal factor in phenomena of plant periodicity which have been regarded by many as explainable only on the basis of an "internal rhythm." This view is strengthened by the fact that definite periodicity in plant development is observable under various climatic conditions, from the equatorial regions to the poles, while the only consistently rhythmic factor of the environment applicable throughout this range is the length of day. In arriving at a correct estimate of the significance of the annual cycle in length of day in regulating periodic plant responses it must be understood that full expression of periodicity is conditioned on the specific requirements of the particular plants in question as to temperature and other environmental factors. The internal mechanism concerned in the marked regulatory action of the length of day on plant growth has not been fully determined, but there is strong evidence that in some way the degree of hydration of the living cell content is brought under very delicate control by the ratio of the number of hours of sunlight to the number of hours of darkness in the 24-hour period.

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PLATE 1

Poinsettia:

The individuals in center and at right are the same plants that are shown in earlier stages in Plate 19, A. Early in September the plant shown at left in Plate 19, A, was transferred to the greenhouse, where it received electric illumination from sunset till midnight in addition to the natural daylight. In response to the lengthened daily light period, the high-colored bracts soon began to assume a green color, particularly in transmitted light. Some of the bracts lost the original red color more or less completely. Finally, a new shoot appeared at the apex of the flowering stem. In the early stages of development this shoot was of the weak, pendent type and the bark of the stem was red. Subsequent development of this stem is shown in Plate 19, B. The plant at right, maintained under long-day conditions throughout the test, continued to develop a vegetative stem. The plant at left received the same treatment as the individual in center, except that the electric illumination from sunset till midnight was omitted. Nothing remains of the inflorescence except the naked stem. Painted from a photograph made January 9.

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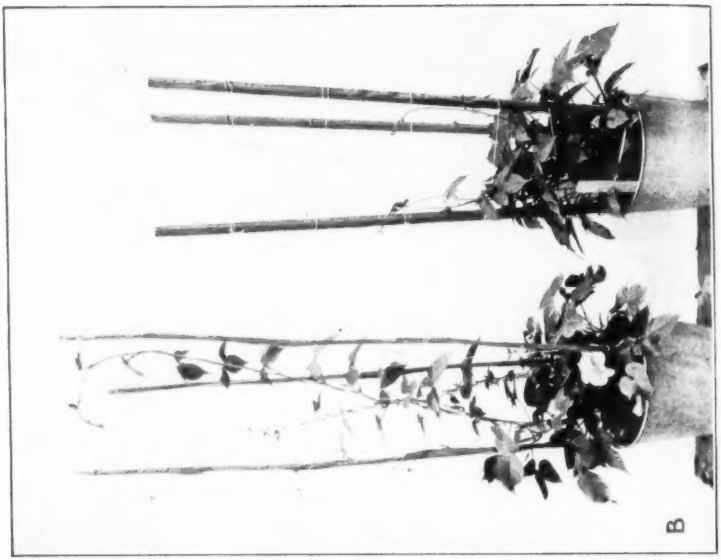
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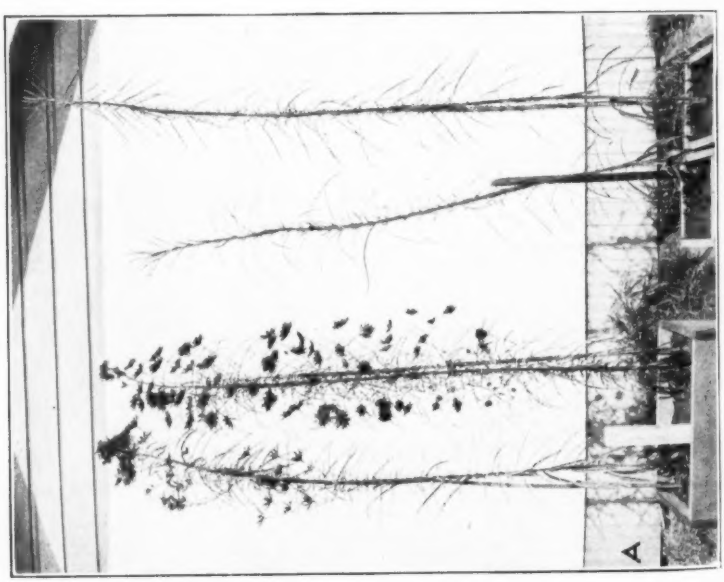
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PLATE 2

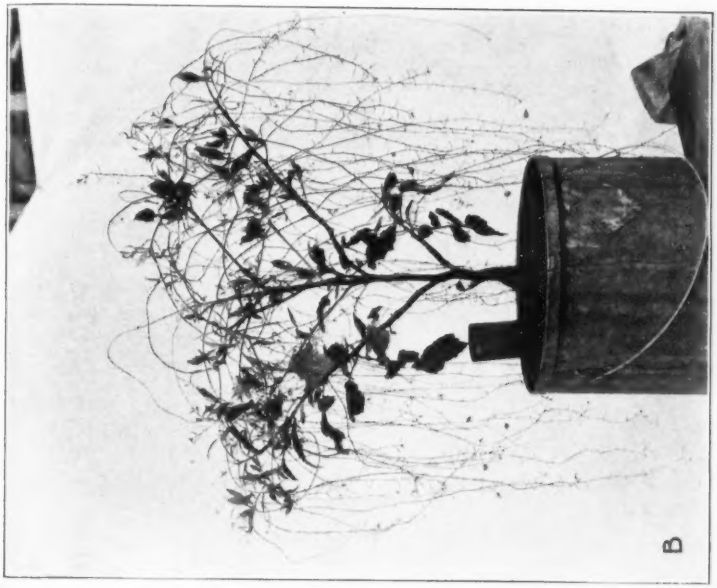
A.—*Helianthus angustifolius* L. Plants at right were exposed to the full daylight period, supplemented with electric light from sunset till midnight, throughout the test, which began January 27. Plants at left were similarly treated till September 2, when they were given a 10-hour daily light exposure. First blossoms appeared on these plants October 4. It is seen that the short-day conditions induced very free flowering and the response was prompt. Photographed October 15.

B.—Morning-glory (*Ipomoea hederacea* Jacq.). Plants from seed which germinated June 11. The first blossom on plant at left, exposed to a 10-hour day from the outset, was open July 10. The first open blossom on plant at right, exposed to the natural length of day, appeared September 9. Photographed July 13.

PLATE 3

A.—Scarlet Globe radish plants, from seeds which germinated May 19. These plants were prevented from flowering by exposure to a day length of only seven hours till October 20, when they were transferred to the greenhouse and allowed to receive the full natural period of daily illumination during the months of November, December and January. By February 1, one of the plants showed evidence of elongating a flowering stem in response to the increasing length of day, and the daily light period was again shortened to seven hours. Elongation of the stem was soon slowed down. It is seen from the photograph that branching is confined chiefly to the upper portion of the stem. The first blossom appeared March 20. Photographed April 17.

B.—Final stages of development of the radish plant shown in A, at right. It is seen that the type of development has been markedly changed by continued exposure to seven hours of light daily. Progressive weakening in power to elongate the primary axis is accompanied by increased transfer of activity to the lower branches. Thus, the effect is to change the general contour of the plant to conform more nearly with that of many woody perennials. It will be observed that the weak, pendent stems which eventually appeared, grew to unusual lengths. These are typical effects of a light period which is markedly suboptimal for increase in stature. Photographed June 2.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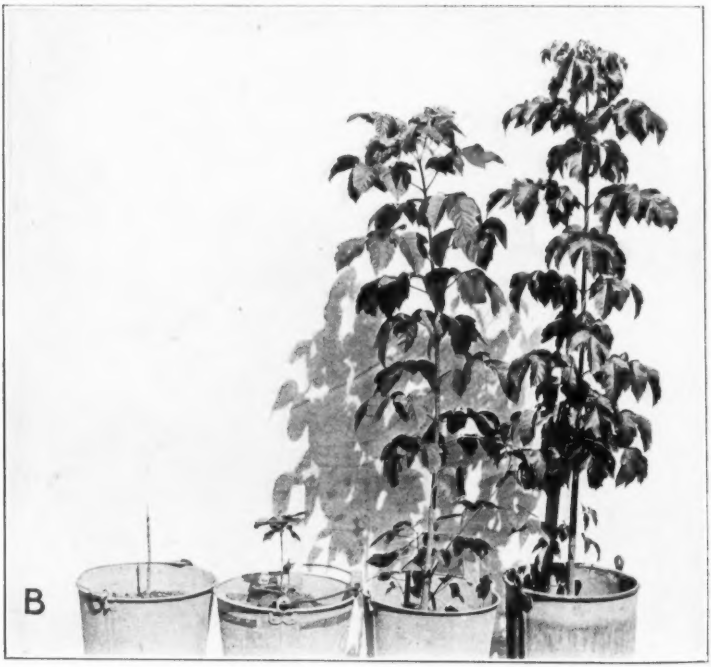
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PLATE 4

A.—Apple seedlings. Plants at right were exposed to 10 hours of light daily during the summer months; those on left received the full daylight exposure of summer. It is apparent that growth is more rapid and vigorous with only 10 hours of light daily than with the 14 to 15 hours of daylight of summer in the latitude of Washington. This would indicate a tendency toward an increased rate of growth with decrease in latitude.

B.—Seedlings of *Acer negundo*. Beginning May 2, the plants at left were exposed to a 10-hour day while the plants at right were exposed to the full day length of summer. It is obvious that in contrast with the apple this species grows vigorously under long-day conditions and could not flourish under the length of day prevailing at Washington during the winter months. Photographed September 22.

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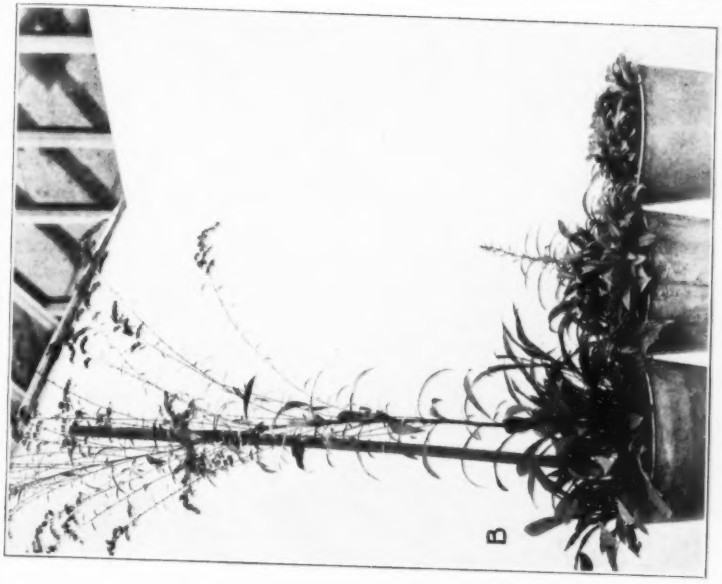
PLATE 5

A.—Grafts of the Baldwin apple, transplanted May 2 and exposed to 12 hours of light daily, beginning May 17. Plant at left is a standard Baldwin while plant at right is a Baldwin graft on dwarf (Paradise) stock. The trees in this series grew vigorously throughout the summer. Only one individual of the control series exposed to the full length of day survived the transplanting. This individual grew very slowly till August, but thereafter there was a marked increase in rate of growth. Photographed September 28.

B.—Goldenrod (*Solidago juncea*). Plant at left exposed to electric illumination during the winter months from sunset till midnight, in addition to the natural daylight. Plants at center and at right exposed to natural daylight only. As indications of initial formation of flowering stems induced by the increasing length of day became apparent on March 10, these plants thereafter were allowed to receive only 7½ hours of light daily. Stem elongation was quickly checked and only the leaf-rosette type of activity was continued.

PLATE 5



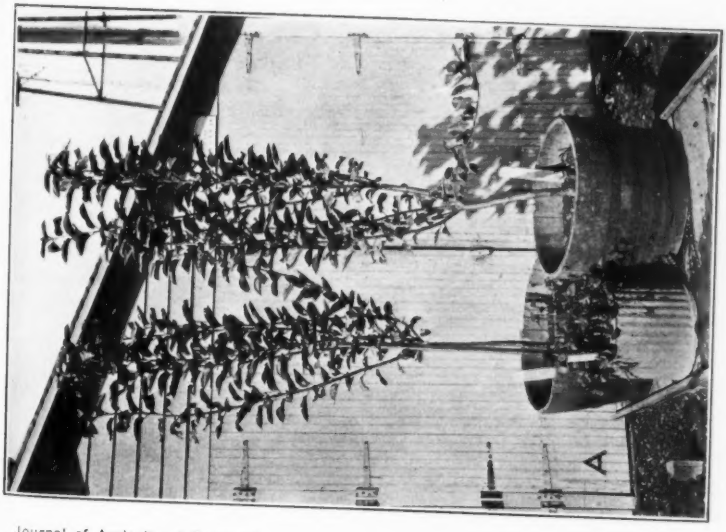


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PLATE 6

A.—Scarlet Runner bean (*Phaseolus multiflorus*). The plants in this series were exposed to the full length of day during the summer and on October 15 were transferred to the greenhouse where they received electric illumination from sunset till midnight, in addition to the natural daylight. Under these conditions there was no tuberization of stem or roots. Photographed January 18.

B.—Scarlet Runner bean plants which were exposed to a 10-hour day till October 15, when they were transferred to the greenhouse and allowed to receive the full natural daylight period of late fall and early winter. Under these short-day conditions there was marked tuberization of the roots while the growth of vines was considerably less than under the long-day conditions. Photographed January 18.

PLATE 7

A.—Tubers of Jerusalem artichoke. The mother plants were grown from tubers which germinated April 25 and were exposed to a 10-hour day from the outset. Although flower buds were formed, they were unable to open. By August 15 the tops of the plants were dead. Tuberization of the underground stems was complete, that is, there was no elongation of unthickened stems. Note the numerous unusually prominent buds on the tubers. Apparently the downward translocation of nutrient materials was so marked as to cut off the requisite food supply of the flower buds. Photographed October 1.

B.—Tubers from control planting of artichoke exposed to the full seasonal length of day. These plants began flowering September 22 and were in full bloom October 1. The difference in tuber formation between these plants and those under a 10-hour day is striking. It is readily seen that under the longer daily light period there was marked elongation of the underground stems and only partial tuberization. The number of new units formed was greater than under the 10-hour day, but they were much smaller in size and showed only inconspicuous buds. In this case the activities of the plant approach more nearly an even distribution between sexual reproduction and tuber formation. Photographed October 1.

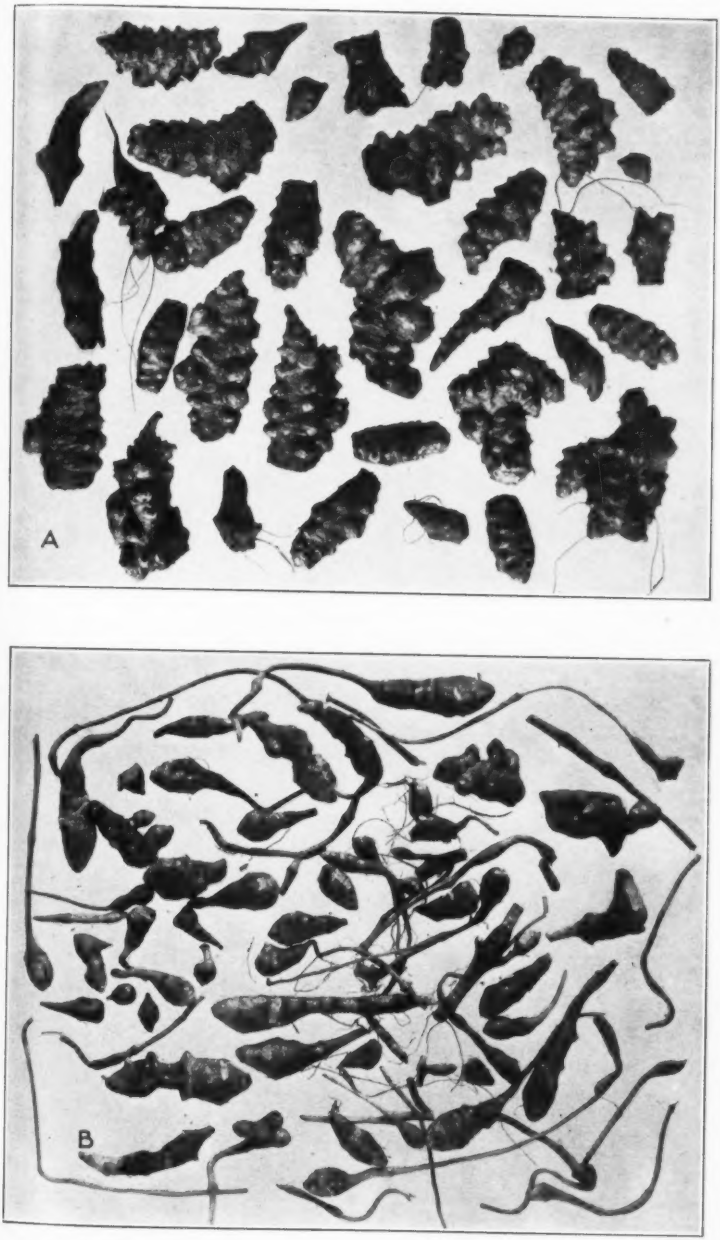
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PLATE 8

A.—Underground portion of Irish potato plant of the McCormick variety. This plant was grown in the greenhouse during the summer months and received electric illumination from sunset till midnight in addition to the natural daylight. No tubers were formed, and while flower buds appeared they were unable to open. Instead of becoming tuberized some of the buds borne on the underground stems at once germinated and formed offsets, thus eliminating the usual rest period. The aerial stems of the mother plant reached unusual heights. As the length of day was progressively reduced there was corresponding increase in tuber formation (see text, page 891).

B.—Plants of table beet, roots of which had been stored in an outdoor pit during the previous winter. Plants at left were exposed to the full seasonal length of day, beginning April 1, and began flowering in June. Plants at right, exposed to a 10-hour day began the development of flowering stems but were unable to flower, the apex of the stem being transformed into a leaf rosette. The branches and leaves are more numerous than under the longer day. Photographed June 14.

PLATE 9

A.—Silverskin onion plants from sets which were planted May 19. Plant at extreme right is representative of a series exposed to the full seasonal length of day in the open air. These plants flowered in July, formed bulbs, and passed through the usual summer rest period after the tops had died down. In the series represented by the second plant from the right, which were exposed to a 13-hour day, the growth of tops was much greater while the bulb was delayed in forming and was reduced in size. The plant in center is representative of those exposed to a 10-hour day. In this case there is no summer rest period and no bulb is formed, the tops remaining green indefinitely. The individual at extreme left shows the behavior of plants grown under the natural length of day in the greenhouse, where the temperature was considerably higher than out of doors. The behavior was the same as that of the controls in the open except that the size attained was materially reduced. With the addition of electric illumination from sunset till midnight in the greenhouse only a slight attenuating effect was observed, as shown by the second plant from the left. Photographed July 28. (Compare Pl. 18, A.)

B.—Biloxi soybeans, showing partial tuberization of the stems in the vicinity of the nodes which results from exposure to a length of day which is too short to admit of free flowering and fruiting. Under these conditions flower and fruit are unable to fully utilize nutritive material reaching them, and these materials are deposited in the surrounding tissues in the more condensed form characteristic of tuberized structures.

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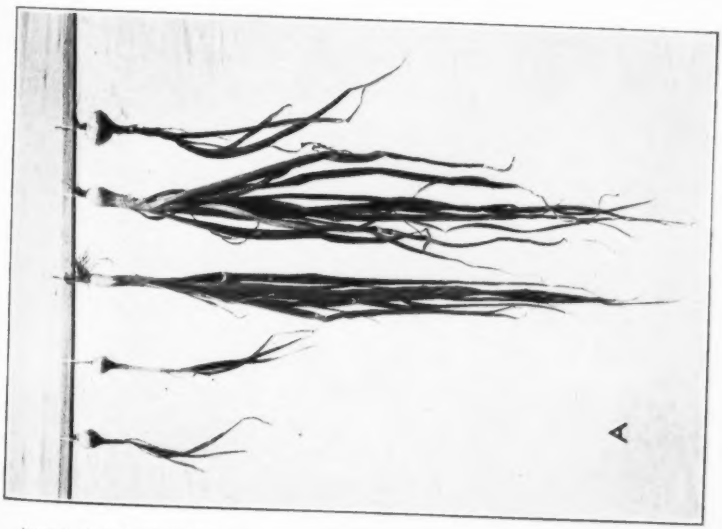
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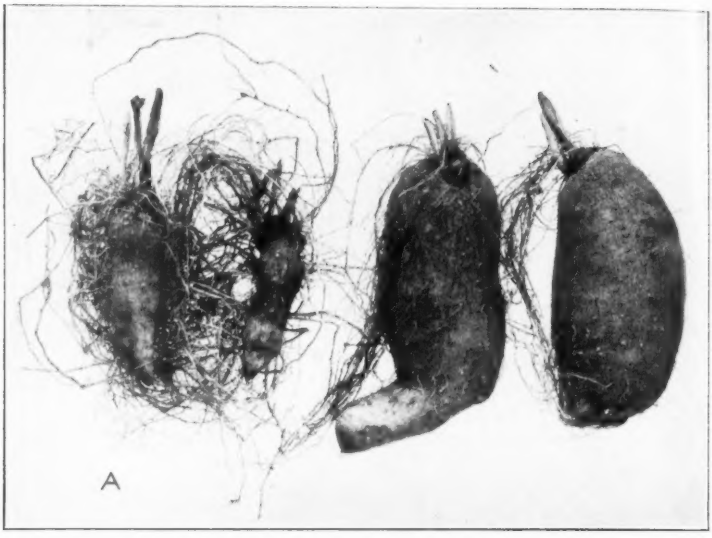
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PLATE 10

A.—Yam (*Dioscorea alata*) from the tropics. Tubers at right are from plants grown under a 12-hour day, beginning May 14, while the tubers at left are from control plants exposed to the full seasonal length of day. The equatorial length of day favors intense tuberization, while the long summer days of high latitudes causes marked development of fibrous roots, with very limited tuberization. The basal flattening of one of the large tubers is the result of "spreading" over the floor of the container in which the plants were grown, suggesting a sort of gravitational settling somewhat like that, for example, of fresh putty. This seems to represent a rather extreme case of loss of capacity for apogeotropic functioning. Photographed October 7.

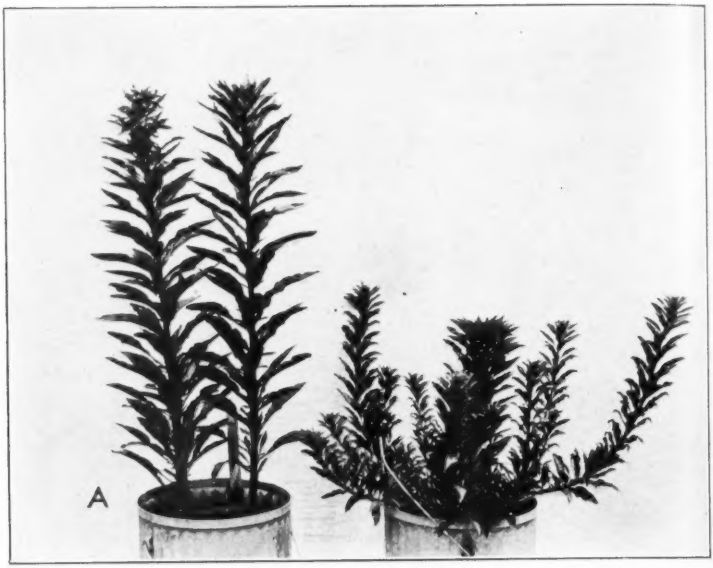
B.—Wild lettuce (*Lactuca spicata*). Plants at left, exposed to a 10-hour day beginning March 29, produced much larger, coarser leaves than the control plants (at right) exposed to the full summer length of day. Under the short-day exposure both leaf and stem were far more hairy than under the long-day conditions. The stature was greatly reduced, but the time of flowering was not affected.

PLATE 11

A.—Honey sorghum, grown in greenhouse and exposed to electric illumination from sunset till midnight during the summer and fall months. Under these conditions branching was confined mostly to the top of the plant. This type of branching resembles that seen in Cosmos at time of flowering and represents an advance toward the sterile, nonbranching type of stem, as compared with basal branching under a shorter length of day. Photographed November 4.

B.—Control planting or sorghum exposed to natural illumination only In this case there is extensive branching at the base, the new shoots developing rapidly and flowering freely.

PLATE II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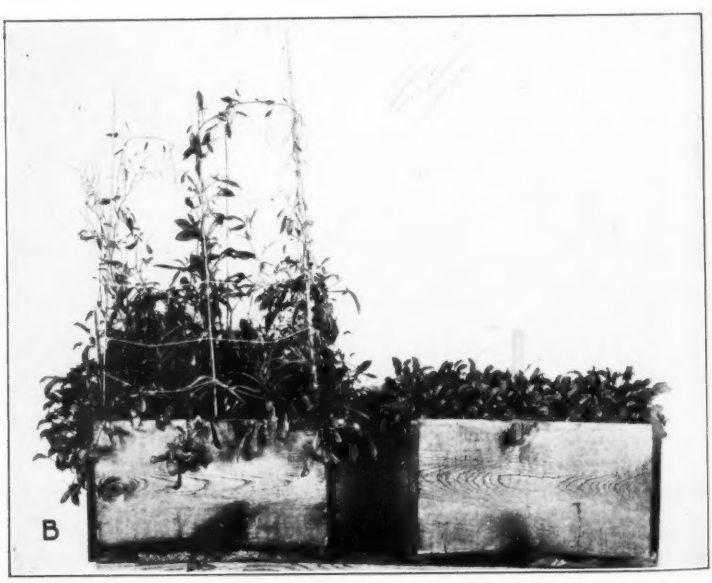
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PLATE 12

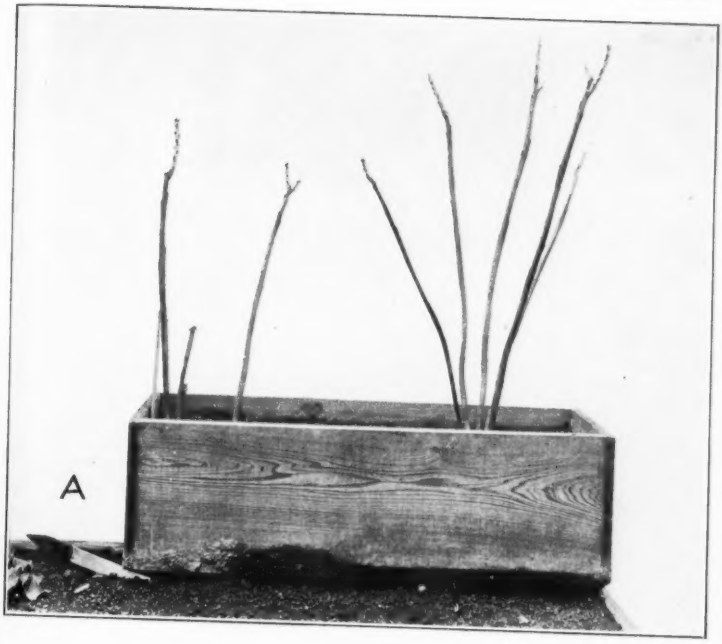
A.—*Oenothera biennis*. Plants at left were exposed to the full daylight period of the spring months. The individual at right received only 10 hours of illumination, beginning March 19. It is seen that the short-day conditions caused a decided weakening in power to elongate the primary axis, resulting in development of numerous basal shoots. In this case dominance of the apical bud is lost, a characteristic response to a suboptimal light period for elongation of the stem. Photographed June 21.

B.—Sorrel (*Rumex acetosella*). Plants at left received electric illumination from sunset till midnight, in addition to natural daylight in the greenhouse, during the winter months. These plants developed numerous aerial flowering stems and in general showed the typical summer behavior of this species. The plants at right, which received only natural illumination, were unable to develop aerial stems but formed thick rosettes of leaves. In reality, however, these latter plants were more active than appearances indicate, for a very large number of underground stems were developed. This behavior of sorrel furnishes further demonstration of the fact that the position, character, and extent of branching are subject to regulation by the length of day. The leaf-rosette form of activity during the fall, winter, and early spring is typical of many plants. Photographed March 25.

PLATE 13

A.—Sumac (*Rhus glabra*). These trees were transplanted in April and remained out of doors till September 8, when they were transferred to the greenhouse. They received the full seasonal length of day throughout the test. The leaves were shed at about the usual time, and the plants remained dormant till spring. Photographed January 11.

B.—Sumac, treated in all respects like the trees in A except that when transferred to the greenhouse in September the trees received electric illumination from sunset till midnight. The leaves were retained through the winter, and, while growth of the original stems was checked, a number of new shoots appeared from the roots about January 1. Photographed January 11.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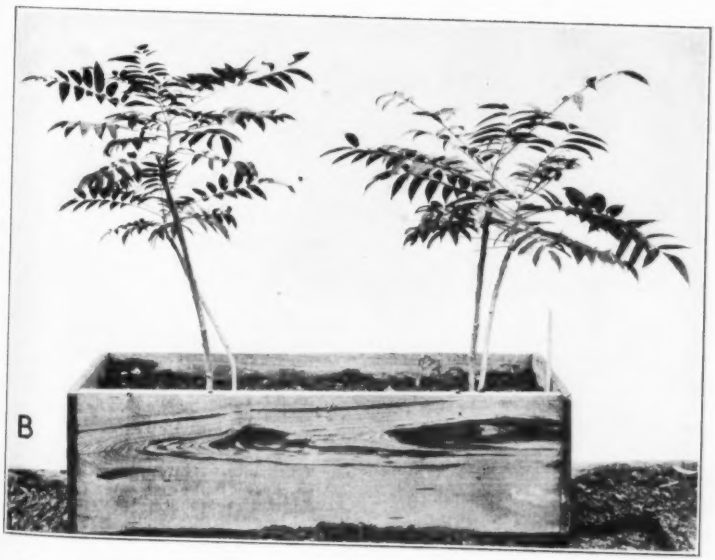
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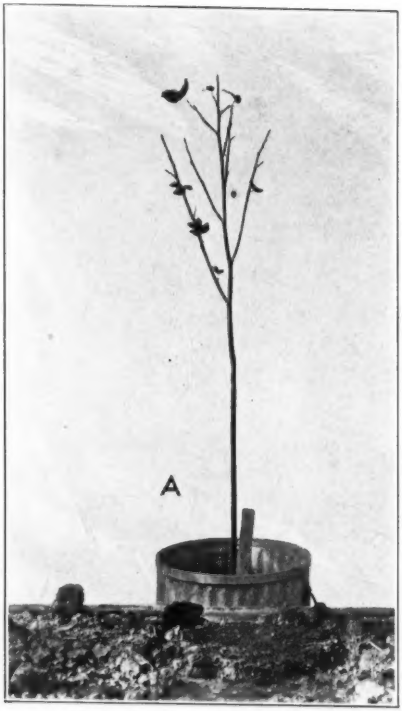
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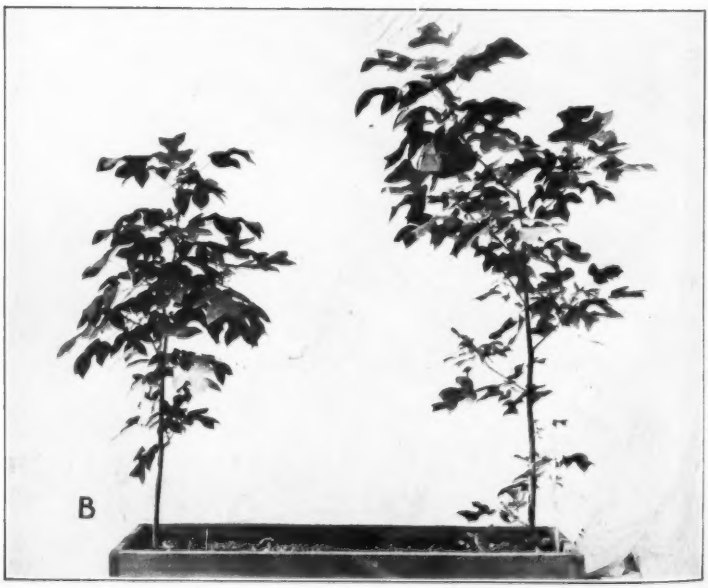
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PLATE 14

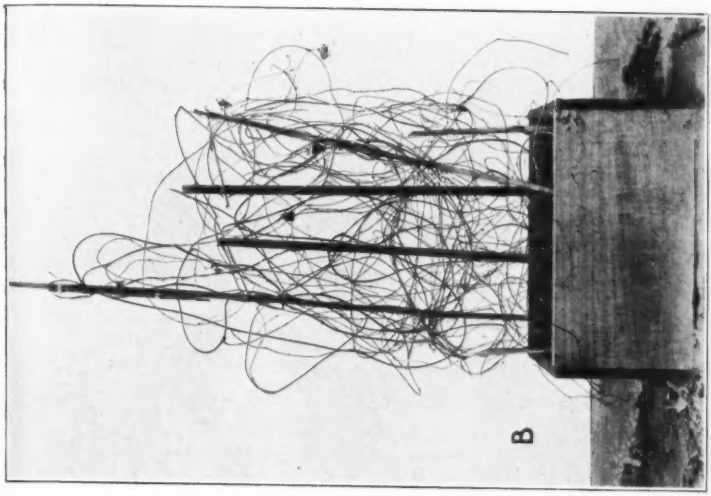
A.—Tulip tree (*Liriodendron tulipifera*), transplanted in April and placed out of doors. On September 8 the tree was transferred to the greenhouse. There was the usual loss of leaves by abscission, followed by dormancy which continued through the winter. Photographed November 18.

B.—Tulip trees, treated in all particulars like the individual shown in A except that after transfer to the greenhouse the trees received electric illumination from sunset till midnight, in addition to the natural daylight. Under these conditions, the rest period was eliminated. Growth was promptly renewed and continued throughout the winter. A characteristic feature was failure to form the absciss layer when old leaves died here and there on the trees. These dead leaves remained firmly attached to the stem, in marked contrast with the usual behavior of this species. Photographed November 18.

PLATE 15

A.—Kudzu (*Pueraria hirsuta* (Thunb.) Scheid.). Seedling which was exposed to a 10-hour day during the summer months. Under these conditions there was little top growth but the basal portion of the stem was moderately tuberized. The plant was transferred to the greenhouse September 15, where it gradually passed into a condition of dormancy which seemed to be fully reached by December 1. The rest period, however, was short and by January 11 new shoots appeared. These shoots grew vigorously, although the leaves were of a darker green than is usual under a longer daily light period. Photographed February 19.

B.—Control seedling of Kudzu treated in all respects like the plant shown in A, except that it was exposed to the full seasonal length of day during the test. In the greenhouse the plant finally lost all leaves and became dormant like the plant in A. Emergence from dormancy was delayed as compared with plant in A, and new shoots did not appear till February 16. Photographed February 19.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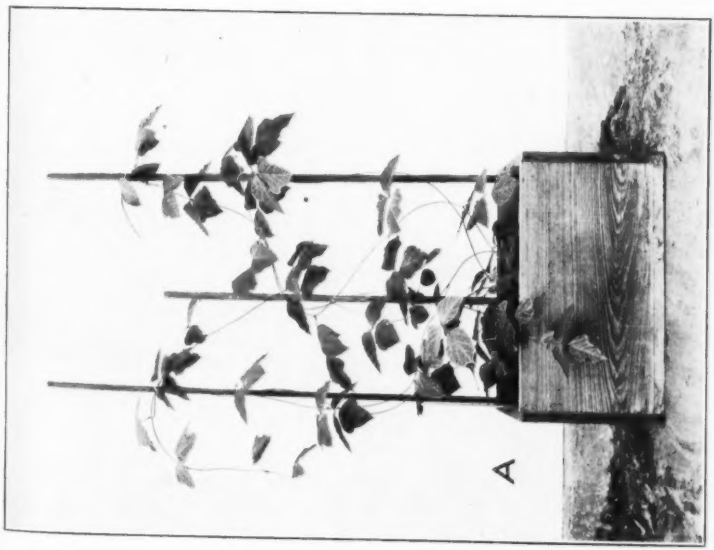
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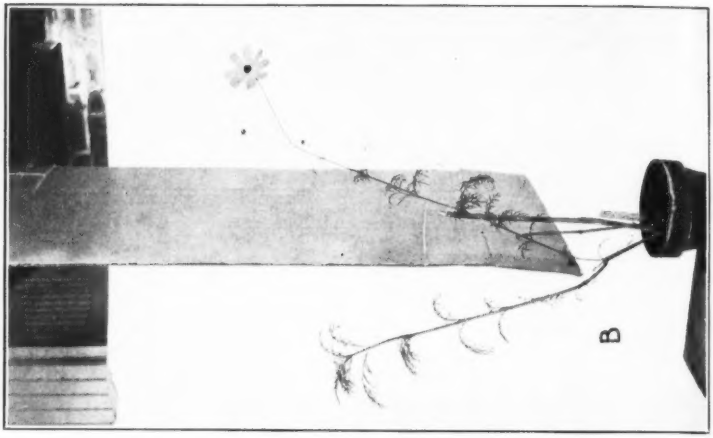
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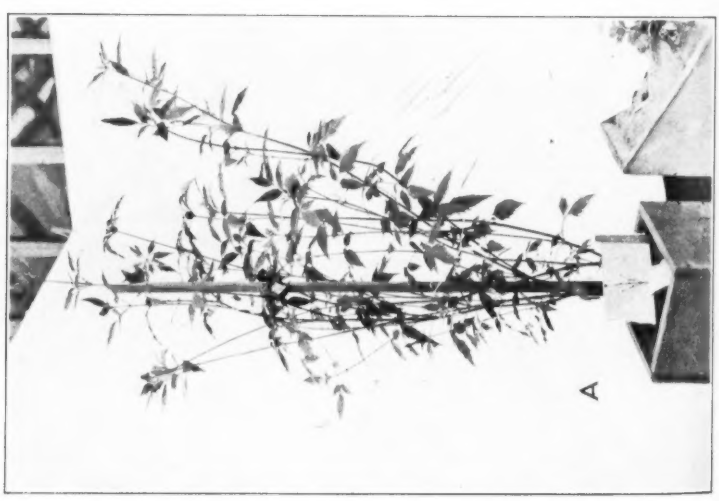
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PLATE 16

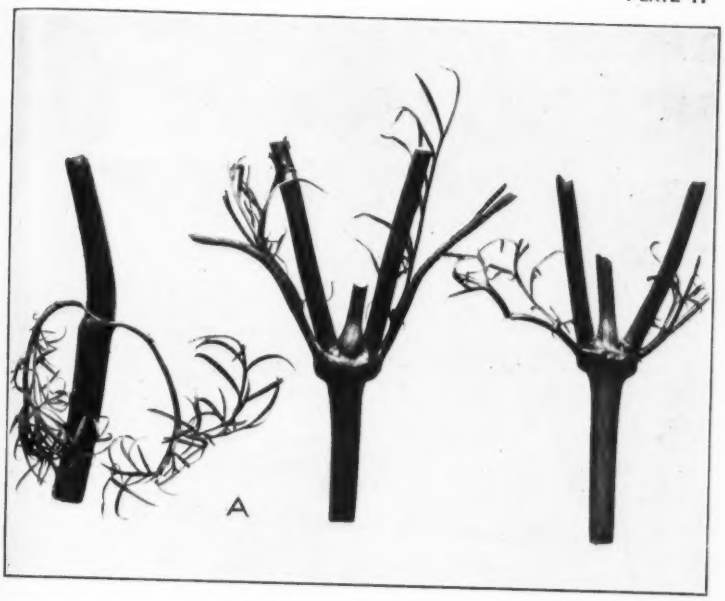
A.—*Bidens frondosa*. Seedling planted in greenhouse; germinated December 23. Beginning January 30, when flowering had begun, the plant received electric illumination from sunset till midnight, in addition to the natural daylight. The total original growth of the plant attained under natural illumination, including ripened fruits, is seen in front of the cardboard. As is shown, this original stem growth died, but new shoots appeared, and these reached giant proportions under the influence of the long daily illumination period. Thus, rejuvenescence was effected by use of a favorable light period. This plant may be regarded as embodying two different types of development at different periods in response to change in the duration of the daily light period. Photographed June 21.

B.—Cosmos. The branch at right flowered promptly in response to the short winter day to which it was exposed, and the usual evidences of advancing senility followed in due course. The branch at left of screen remained sterile and continued to grow in response to the added electric illumination from sunset till midnight. The dominant influence of this branch over the flowering branch in its effect on basal portions of the plant is evident. In this instance two different types of development take place simultaneously on the same plant in response to difference in the light period (compare with A). Photographed March 25.

PLATE 17

A.—Stems of Cosmos, grown in winter in greenhouse. Electric illumination was used from sunset till midnight as a supplement to the natural daylight. Sections of stems in center and at right show the effects of cutting back in causing local swelling of the nodes, followed by development of new branches. This behavior indicates a strong upward flow of sap from below, resulting from exposure to a length of day favorable to elongation of the vegetative stem. This behavior is not observed when the plant is exposed to short-day conditions. The section of stem at left illustrates the condition of the nodes at the time cutting back was done.

B.—*Hibiscus moscheutos*. Seedlings of previous summer's growth which remained out of doors during the winter. Beginning March 27, the two plants at left were given a 10-hour day while the control plants at right continued to receive the full seasonal length of day. Under the 10-hour day small, weak basal shoots finally appeared in May, as seen in front of the cardboard. These shoots were unable to grow and soon perished. New shoots appeared on the controls early in April, and these continued to develop normally. Photographed June 21.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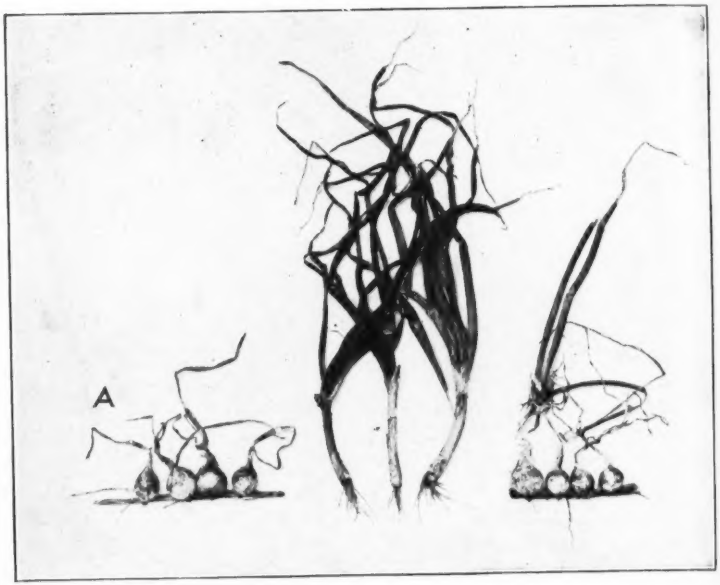
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PLATE 18

A.—Silverskin onions, grown with different conditions of light intensity and with differences in the length of the daily light period. The plants at left were exposed to full intensity of the sunlight for the entire day. Plants at right were exposed to sunlight for the entire day, but the intensity of the light was reduced to a third of the normal by means of a cheesecloth shade. The plants in the center were exposed to the full intensity of the sunlight, but the duration of the daily period of illumination was reduced to 10 hours (5.30 a. m. to 3.30 p. m.). It is easily seen that the strong reduction in intensity of the light has had but little effect on bulb formation and entrance into the summer rest period. Shortening the length of day by less than a third (and thus reducing the total radiant energy of the sunlight received by a far less proportion), however, has effectively prevented the formation of bulbs and the appearance of the summer rest period.

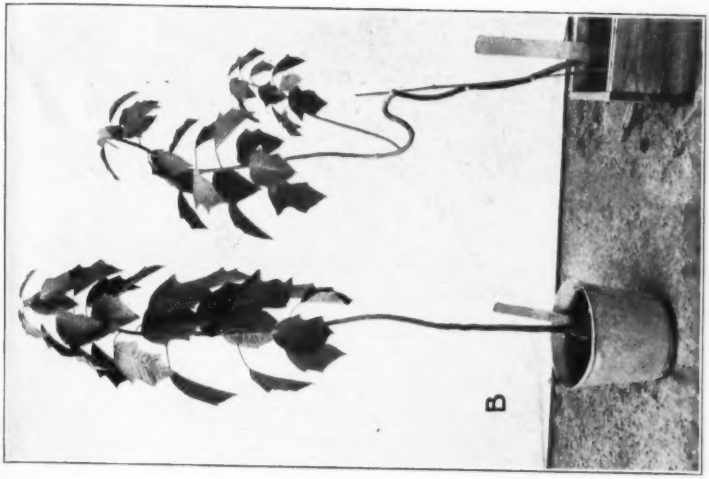
B.—Violet. Plant at left in flower shows the characteristic behavior under the relatively short days of spring and fall. The plants in the center and at the right were exposed to electric light from sunset till midnight as a supplement to winter daylight. Beginning January 30, however, the daily light period of the center plant was reduced to 7½ hours. In a few days there was partial loss of turgidity in the leaf stems, resulting in the prostrate condition to be noted in the photograph. Subsequently the characteristic blue blossoms of spring appeared in this plant. This experiment seems to suggest that permeability of the plasmic membrane or the degree of dydration of the protoplasm is affected by the length of day. This prostrate type of development is a characteristic feature in the development of many plants under short-day conditions. Photographed April 17.

PLATE 19

Poinsettia:

A.—Beginning July 9, the plant at left was exposed to a 10-hour day. Before the close of August this plant had flowered and was richly colored. The control plant at right, exposed to the seasonal length of day, of course, did not flower till early winter. This experiment is of interest in showing that the green chlorophyll pigments of the leaf may give way to other pigments with appropriate change in the light period. Photograph made September 13.

B.—In the plant at right can be seen the completed rejuvenescence effected in the weak, pendent shoot which appeared at the tip of the stem bearing an inflorescence, as shown in Plate 1. This rejuvenescence was accomplished by exposure to a daily illumination of about 18 hours, after flowering had been induced by exposure to a 10-hour day as shown in Plate 19, A. The U-shaped portion of the woody stem resulted from the pendent position of the new shoot as it first appeared. The short horizontal section of stem is that on which the inflorescence was borne. Plant at left illustrates the tall, spirelike development of the stem, absence of branching, and progressive loss of lower leaves which yield their plastic nutrient materials to the upper plant parts, all of which are typical features of the response to a long day. Photographed July 13.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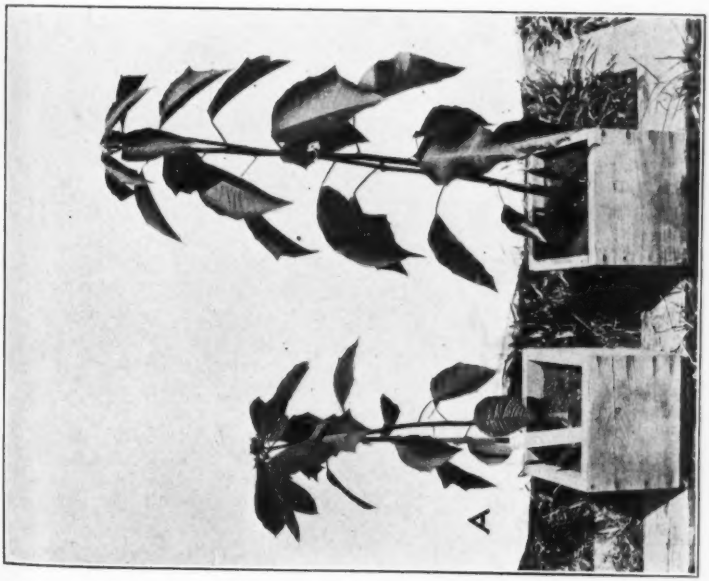
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AGAMERMIS DECAUDATA COBB, STEINER, AND CHRISTIE; A NEMA PARASITE OF GRASSHOPPERS AND OTHER INSECTS.[1]

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INTRODUCTION

This is a preliminary account of a joint investigation carried on at Washington, D. C., and Falls Church, Va., and relates to a nema *Agamermis decaudata*, parasitic in insects, particularly in Orthoptera. The work at Falls Church is carried on with the cooperation of the Bureau of Entomology at its eastern field station, and all the insects examined have been determined by officers of that bureau. Other valuable assistance has been rendered by approximately 150 American zoologists and entomologists, whose aid has made possible a first tentative map of distribution of the parasite in the United States.

The general oversight of the work has been handled by the senior author, who has given special attention also to methods and apparatus, and to the structure and behavior of the free-living larva. Dr. Steiner gave special attention to the structure and taxonomy of the parasitic and post-parasitic stages. He has also handled nearly entirely the difficult matter of the literature and nomenclature. Prof. Christie has given special attention to field and laboratory work connected with the hosts and their habits, the effect on the host, the habits and distribution of the post-parasitic forms in the soil under natural conditions, and to the rearing of both host and parasite.

In the present account it is not proposed to do more than sketch some of the main features of the work, which has involved thousands of dissections, hundreds of carefully executed laboratory and rearing experiments, and the invention and trial of dozens of different pieces of special apparatus adapted to various features of the work.

A broad numerical basis has been given the facts disclosed, since the work has for its definite object the economic application of the data secured. The summary presents two aspects, the latter of which is subdivided: First, the results show positively that, in certain cases believed to be typical, the nema *Agamermis decaudata*, is an important factor in the birth rate of certain injurious insects; second, the application of this fact may be exploited in two ways, (*a*) by colonization—that is, moving the parasite from places where it exists to places where it does not exist, or is rare; the experiments show that this can be done, either by transferring diseased insects, such as grasshoppers, or by transferring the parasite itself in one form or another; (*b*) by forecast—since methods of detecting the parasite have been developed to a point where it is believed possible to hazard some form of prediction. Just as, if we can not control the weather, it is at least important to be able to predict it, so, if we can not prevent the ravages of an insect, it is at least important to be able to predict when the ravages are likely to occur. In this respect the results of the investigations are considered positive.

[1] Accepted for publication Mar. 7, 1923.

SOURCES AND DETERMINATION OF THE NEMAS

In the main the material for these investigations was collected at Falls Church, Va., but questionnaires were sent to zoologists all over the United States. Nearly 160 of these were returned, some with collected Mermithid material, and many with very interesting information about distribution, hosts, etc.

The examination of this contributed material is not yet finished, and therefore no more than a somewhat brief sketch of the American Mermithid land-fauna can be given, together with some aspects of the economic value of the family.

On leaving the insect host the nemas enter the soil. There have been observed thus far a dozen or more species of Mermithids from American soil, mostly new. The two most common are what have been called *Mermis albicans* Von Siebold and *M. nigrescens* Dujardin, which are among the first Mermithids made known and also the ones most frequently mentioned in literature. Both apparently have a wide geographical distribution.

The determination of Mermithid species is difficult; one reason is that often only larval forms are obtainable, and another is that Mermithids do not possess obvious morphological characteristics. The present studies were much aided by the excellent papers of Meissner (*5*, *6*),[1] Rauther (*7*), and Hagmeier (*3*). The latter emphasized the opinion that among the principal and best aids in classifying Mermithids are the sense organs on the head, since they rarely change during the life of the individual.

Whereas *Mermis nigrescens* seems to show little variation and to be represented in this country by the typical European form, the American *Agamermis decaudata* is unusually difficult of determination, even for a Mermithid, because it presents an extensive series of variations, between the extremes of which there is a complete gradation of intermediate forms. These varieties, or races, and apparent hybrids are best recognized by the structure and arrangement of the head sense organs. As far as can be judged, the European *albicans* as described by Meissner (*5*, *6*), Rauther (*7*), and Hagmeier (*3*) has not yet been found in this country. The chaos of these forms is probably greatly augmented by hybridization. Cases occurred at Falls Church where the mating female and four males (four males with one female) all differed in the structure of the head sense organs.

Another interesting evidence of the existence of a number of different races in *Agamermis decaudata* is the fact that almost any collection that includes a number of female specimens will show intersexes—that is, females with more or less well developed male sexual organs. Experimental biology is showing that such intersexes may be frequent in the "artificial" crosses of closely related forms, races, or genotypes. *A. decaudata* as it occurs in nature, is not a clean-cut species, but rather a mixture of races and their hybrids.

The origin of the races of *Agamermis decaudata* is still uncertain. Perhaps the great variety of hosts may have some influence.

It may be considered questionable whether there are *decaudata* races special to certain hosts. We do not know yet, but it appears as if larvae of various races are entering hosts without special choice.

[1] Reference is made by number (italic) to "Literature cited," p. 926.

A review of the information obtained from the returned questionnaires also emphasizes the economic value of Mermithids, a fact surmised earlier by a number of entomologists but never proved in a substantial way. Of 130 returned questionnaires, 53.6 per cent state that Orthoptera were the hosts. In 51 cases the writers made observations regarding the effect of the parasite, mostly on an individual host. Of these latter observers, 85 per cent report an injurious effect on the host, 71 per cent stating that the normal development of the host was prevented, 47 per cent stating the fecundity of the host was reduced, and 53 per cent that the host was killed. Most of these statements seem mainly the result of fortuitous observation on a limited scale; in general, they corroborate those already mentioned in the literature. Hagmeier (*3*) estimated that on a meadow 33 per cent of all grasshoppers were infested with Mermis; Glaser and Wilcox (*2*) in this country estimated infestation up to 60 per cent; Leidy (*4*), very frequent; Steiner's observations (*8*, *p. 223*) showed in a garden heavily infested with the snail *Limax agrestis*, 20 to 30 per cent of them mermithized.

EXPERIMENTS AT THE EASTERN FIELD STATION OF THE BUREAU OF ENTOMOLOGY AT FALLS CHURCH, VA.

During the early part of July, 1922, it was noticed that grasshoppers in the vicinity of Falls Church, Va., were infested by a Mermithid parasite. From that time until cold weather, collections were made over an area of several square miles, and a total of 3,332 grasshoppers was examined. Of the 824 Tittigonidae included in this number, very nearly all were *Orchelimum vulgare* Harris. Of the remaining 2,508 Acrididae, about 90 per cent were *Melanoplus femur-rubrum* Deg. Mermithid infestation was found to average 12 per cent, increasing to about 25 per cent in heavily infested regions.

Records based on the examination of 2,498 grasshoppers, the sexes of which were determined before dissection, show the males and females to be about equally parasitized.

As the nemas do not reach sexual maturity in the host, but moult once in the soil after leaving the host, the determination of the material taken from grasshoppers is a difficult task. However, it is certain that the greater number of the nemas were varieties or races of *Agamermis decaudata*, with an occasional species of another kind.

The parasites begin to leave the hosts by the latter part of August, if not before, and are nearly all out by the first of October. Their method of exit is by forcing their way through the body wall of the insect. In one carefully observed case the parasite issued from the side of the abdomen, head foremost, and was free in a very few minutes. The parasite was assisted by the kicking of the grasshopper, whose feet became entangled in the coils of the nema.

Once free from the host, the Mermithids make their way into the soil to a depth of 3 to 20 cm. The females go down from 4 to 8 cm., seldom deeper. Here they coil up in the "nest," forming a "knot," and apparently never again move about. The males move through the soil more freely, as it is evidently their function to seek out the females. The "knots" as dug from the soil during the winter contain one female, rarely more, and from one to seven males.

In order to determine the approximate Mermithid population in an infested region, 16 square feet of soil were examined to a depth of 30 cm. (12 in.). The yield was 132 Mermithids, or at the rate of 359,370 per acre.

Eggs are laid in large numbers until both the nemas and the wall of the nest become plastered with them. Egg counts show that each female lays, on an average, at least 5,000 eggs. Under the 16 square feet referred to in the preceding paragraph, 32 "knots" were surrounded with eggs. If the average number of eggs per nest is 5,000 (probably a very conservative figure) there will be, provided all the eggs hatch, 435,600,000 larvae per acre. Each foot will therefore support a population of 10,000, and each square inch of surface will have below it about 70 of these young Mermithids

The egg has the shape of a slightly flattened sphere, and measures 119 by 105 microns. The rate of its development is influenced by external conditions, particularly temperature. At the end of five or six days, with average September weather, the embryo takes the form of a single, circular coil, almost filling the shell. At this point in its development there is a rapid proliferation of cells at the posterior extremity, the ends of the loop overlap and in a short time several coils are developed. As the length of the embryo increases new coils are formed until, at the end of about a month, the young larva reaches its full length of a dozen or more coils—that is, 3 to 4 mm. The development of eggs deposited late in the fall seems to be retarded by cold weather, for material collected in March still contains the earlier stages of development. The hatching of the eggs is probably brought about by the warm spring weather, as eggs brought into the laboratory in winter and kept at room temperature hatch freely after three or four days.

After hatching, the larvae work their way to the surface of the soil and enter the newly hatched grasshopper nymphs.

Artificially infested grasshoppers containing six or eight Mermithids die in about eight days. In fact it may be doubtful if grasshoppers harboring more than one parasite ever reach maturity. The ovaries of infested females which do survive are vestigial, never producing functional eggs, and it is likely that the males are also rendered sterile. The exit of the nemas, sometimes at least, results in the death of the grasshopper, and there is every reason to believe that this is always the case.

STRUCTURE AND BEHAVIOR OF THE FREE-LIVING LARVA

The rear five-sixths of the *decaudata* larva has a certain uniformity of structure. Here the cuticle and body wall are typically nemic. The body cavity is filled by a moniliform series of elements, having somewhat the general character of nemic intestinal cells, but there is no lumen and no trace of an anus. Each of these 50 to 70 cells (trophocytes), in addition to its nucleus, protoplasmic network, and minute proteid granules, is packed with spherical 3–4 micron fat globules, melting at about 55° C., and contains a thin-walled catabolic vesicle holding a birefringent crystal. As the larva ages, the fat disappears, while the vesicle increases, thus pushing all other contents of the cell to one end. In a few weeks no fat remains, and the nema has a segmented aspect. By expending the fat of the trophocytes, the posterior five-sixths of the nema becomes the active mechanism for driving the strongly cephalated anterior sixth to, and into, the host.

On entering the host the driving mechanism is shed at a predetermined, elaborately prepared node, and only the cephalic portion becomes parasitic. The node at which this automatic amputation takes place is prominent in the free-living larva. Persisting as a little altered terminal scar, it indicates that no moult occurs during the parasitic life. Usually

the driving mechanism is left outside the host, but young larvae in which the node is unripe may take the driving mechanism inside, where, in the course of a few days, it is shed. The nema requires from two to five minutes to enter the host. This period is often preceded by a few minutes of waiting—perhaps devoted to some internal preparation for the onslaught. Entrance is bored at any thin part of the cuticle of the very young larva of the host—namely, on the head, thorax, abdomen, or legs.

The cephalic end of the free-living larva is highly specialized. No particular reference is made here to its acute, hollow, protrusile spear, or its six inconspicuous cephalic papillae, amphids, nerve-ring, oesophageal lumen, and longitudinal chords,[3] most of which closely resemble those of the "*Mermis albicans*" of Hagmeier. The bifurcated, symmetrical, two-celled renette lies in the neck behind the nerve-ring. The oesophagus ends posteriorly in a short, small, cylindroid swelling, which at intervals of about a second may exhibit the sudden peristaltic motions characteristic of the swallowing act of nemas.

The intestine comprises two sections, of which the posterior is about two bodywidths long. The four times longer anterior section, comprising sixteen cells, has a distinct, narrow, refractive, tubular lumen, and is flanked by three unequal glandular structures having their free ends caudad, the largest of which, the right, extends throughout the length of this section of the intestine, while the two others—equal, narrower, and on the left—have only half that length. These organs are packed with minute dodecahedral, colorless, in the main nonstaining (carmine, osmic), refractive granules, of which those in the largest organ are very much the largest; beside this, there are physiological differences, in that the two smaller organs stain differently intra vitam from the large one and behave differently after the larva enters its host. During the early days of parasitism these three organs disappear, so they evidently have to do with the physiological changes connected with the inception of taking in food from the host. The intestinal lumen in the 20–30-celled posterior section is of a different, nonrefractive character (wider and surrounded by a very thin nonrefractive wall), and this section presents the elements commonly seen in the intestinal cells of free-living nemas.

The sexual blastomeres nearly always lie in the axil between the two portions of the intestine.

After entering the host the posterior portion of the intestine changes and gives rise to a syncytiumlike (?) structure of relatively enormous size. As the three glandular organs disappear, the anterior 16-celled section of the intestine also begins a relatively huge growth, at first (20 days) forming a somewhat moniliform series of 16 organs (urocytes?) with large nuclei very like the four organs of *Tetradonema* (*1*). The early growth of the two portions of the intestine is not so very unequal, so that the sexual anlage comes to lie nearer the middle of the body. Along with this enormous growth of the intestinal elements the longitudinal chords,[3] especially the lateral, increase greatly in volume from back to front.

In spite of the fact that the free-living *decaudata* larvae will live for hours or even days on thawing ice, when placed in water or moist earth at 32° F. they are much injured by the congealment. Two or three such experiences kill them. One exposure to zero Fahrenheit kills them. It seems probable that they can not survive even light frosts in nature.

[3] Hitherto usually referred to in the literature as the "longitudinal fields."

These free-living larvae can exist in soil for several months, during which time experiments have shown them to be apogeotropic and positively phototropic, rheotropic, pedotropic,[4] and xenotropic.[5] Within the limits of the vernal temperatures of arable soils in subtemperate regions, the larvae are positively thermotropic. Once dried they die.

From what has been previously said concerning the deposition of the eggs, it will be seen that these tropisms tend to bring the larva to the surface of the ground and into contact with its host.

The entrance of the larva into its host, although very easily brought about in the laboratory, has not been observed in nature and doubtless will be a matter very difficult of observation. The forecast is that the larvae will come to the surface of the ground in late spring, leave the soil, lurk among the decayed and living vegetation near the surface of the ground, and enter the host mostly at night.

The bobtailed parasitic larva, 25 by 700 microns, grows at a rapid rate, often increasing a millionfold in two to three months.

BRIEF GENERIC AND SPECIFIC DIAGNOSES[6]

Agamermis Cobb, Steiner, and Christie n. gen.

Mermithidae with terminal mouth, no mouth papillae, 6 head papillae, vagina S-shaped, 2 spicula; parasitic larva decaudate. Moults once in the egg.

Agamermis decaudata Cobb, Steiner, and Christie n. sp.

Characters as given on pages 924–926 herein, and as shown by Hagmeier's figures (except fig. 14) for his *Mermis albicans* (3). Amphids, however, varying somewhat from those figured by Hagmeier; no cervical papillae seen. Moults once in the egg.

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[4] γῆδος = soil.
[5] ξένος = host.
[6] Full descriptions will be published later.